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**The effects of terrigenous sediment on the behaviour of
Macomona liliana (Bivalvia) in permeable sediments:
Implications for porewater exchange.**

A thesis
submitted in partial fulfilment
of the requirements for the degree
of
MASTER OF SCIENCE IN BIOLOGICAL SCIENCE
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ABSTRACT

Catastrophic sedimentation events create one off disturbances that can cause mass mortality events in receiving estuaries. In contrast, the deposition of small amounts of terrigenous sediment (TS) is on-going and likely to have long-term consequences for benthic communities who, play important roles in ecosystem functioning. The aim of this thesis was to look at the effects of small amounts of TS on the behaviour of an infaunal deposit-feeding bivalve (*Macomona liliana*), which may have implications for sediment porewater fluxes and ecosystem functioning. To determine the effect of TS on behaviour, mesocosm experiments in a recirculating flume tank were run. Time lapse imagery was used to capture surface activity, and high resolution pressure sensors were buried within the sediment and captured changes in hydraulic activity. The effect of three TS treatments were tested, low, high and mixed. The low and high treatments were surface additions of TS (0.09 g cm^{-2} and 0.20 g cm^{-2} , respectively) and represented the initial deposition and build-up of TS. The mixed treatment, mixed 0.20 g cm^{-2} through the top 2 cm of sediment, to mimic the incorporation of TS into marine sediments over time. Behaviours were observed pre- and post-treatment addition, and were compared to determine the effect of TS on *M. liliana* behaviour. The surface (top 2 cm) sediment properties were measured to determine the degree of surface modification by the TS treatments.

TS significantly modified the properties of the sediment surface and the hydraulic conductivity. These caused subtle, but significant, changes in some of the behaviours observed in *M. liliana*, and on a whole, behaviour which bioturbated the sediment surface decreased. Two feeding modes were observed at the surface, deposit-feeding and suspension-feeding/ventilation. There was a switch in feeding modes, from deposit-feeding to suspension-feeding/ventilation, in the low and mixed treatments. The duration of suspension-feeding/ventilation was, on average, three times longer than deposit-feeding, across all treatments, therefore a switch in modes altered the temporal patterns of sediment pressurisation. The amplitude of sediment pressurisation during feeding was significantly increased in the mixed treatment (up to $5\times$ higher) as a result of decreased hydraulic conductivity. Additionally, the pressure signal measured

during deposit-feeding was twice that of suspension-feeding/ventilation in the mixed treatment.

Collectively the short-term changes in *M. liliana* behaviour are likely to increase sediment stability and the persistence of TS in the environment, potentially causing long-term degradation to habitat and *M. liliana* condition. As a result of reduced hydraulic conductivity, larger porewater fluxes are likely to be generated in the mixed treatment, and this would be two fold larger during deposit-feeding than in suspension-feeding/ventilation. This paired with the different temporal scales of the two feeding modes, and the observed switches in feeding modes, would have important consequences for geochemical conditions. Rather than short periods of high pressurisation, there would be longer periods of smaller pressurisations, which would increase the duration of sediment oxygenation, but reduce the porewater flux. This is likely to promote more stable geochemical conditions, which when compared to oscillating conditions, has been shown to reduce nutrient recycling and estuarine productivity.

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CHAPTER ONE: INTRODUCTION

1.1 Estuarine ecosystem functioning

Estuaries represent a zone of transition between terrestrial, freshwater and marine environments (Pritchard 1967). In New Zealand, barrier-enclosed lagoons are widespread (c. 65 out of a total 300) (Jones et al. under review). These estuaries have extensive intertidal flats, with a tidal prism that makes up a large proportion of total estuary water volume (Hume et al. 2007) and are arguably one of the most productive ecosystems in the world (Orfanidis et al. 2001). The shallow water depth and often low turbidity means that light is not limiting and the release of nutrients recycled in the sediments are readily available to communities of microphytobenthos (benthic microalgae). The microphytobenthos contribute significantly to primary production in shallow waters (Gargas 1972; Nowicki and Nixon 1985; Varela and Penas 1985; Plantecuny and Bodoy 1987; Jassby et al. 1993; Macintyre and Cullen 1995) and dominate the productivity of intertidal habitats (Joint 1978; Varela and Penas 1985). This benthic productivity supports diverse estuarine and coastal communities (Haese and Pronk 2011; Jones et al. under review).

Shallow estuaries provide crucial economic, cultural and ecological goods and services (Levin et al. 2001), defined as “the direct and indirect benefits people obtain from ecosystems” (Beaumont et al. 2007, pg 254). For example, New Zealand’s seafood industry harvests about 600,000 t yr⁻¹ from wild fisheries and aquaculture which at some level is supported by estuarine productivity (Ministry of Primary Industries 2012). Salt marshes, mangrove forests and sea grass beds in estuaries also dampen and prevent the impact of tidal surges, storms and floods (Davison and Hughes 1998) (see Figure 1 for more examples).

The functioning of shallow estuaries is dependent on exchange of particles and solutes between the benthic and pelagic environments (benthic-pelagic coupling) (Kelly et al. 1985; Nixon et al. 1996). Benthic-pelagic coupling governs the exchange of organisms, the availability of oxygen in the sediment, the recycling of organic matter and the subsequent release of nutrients back into the water

column, where it is available to primary producers (Blackburn 1988). The disruption of benthic-pelagic coupling can lead to shifts in ecosystem functioning (Rodil et al. 2011).

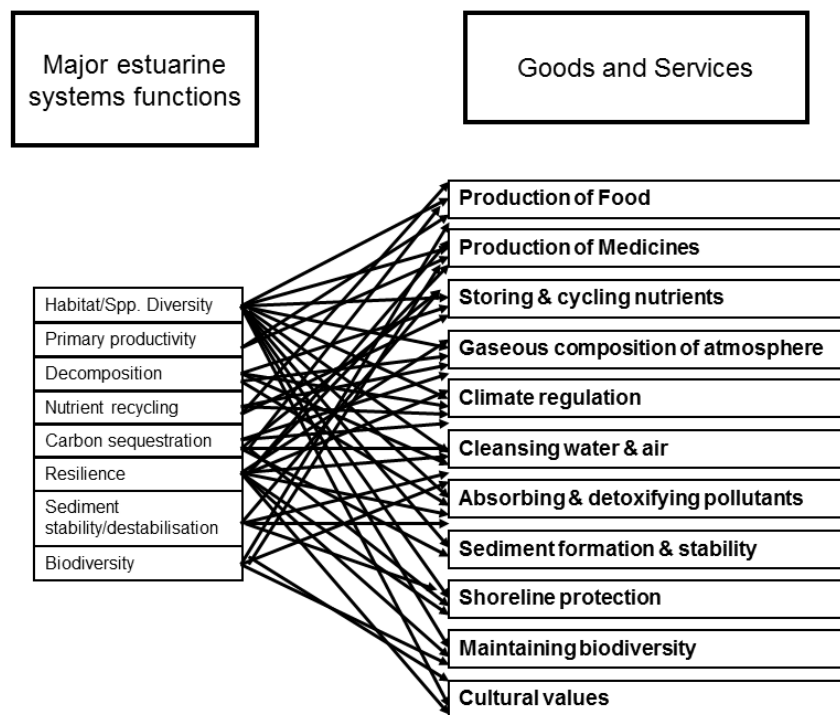


Figure 1: Multi-ecosystem functionality and the relationships with a broad range of ecosystem services (Townsend et al. 2011).

1.1.1 Threats to ecosystem functioning

Around the world, estuaries are threatened by a range of anthropogenic perturbations that stem from overpopulation, land use changes and development in catchments, as well as activities within estuaries themselves. Threats include; pollution (Bonsdorff et al. 1997), fisheries exploitation (Jennings and Kaiser 1998), introduced species (Cohen and Carlton 1998), freshwater diversions (Kimmerer 2002), shoreline development (Seitz et al. 2006), dredging (Kaplan et al. 1974) and increased sedimentation (Turk and Risk 1981). These stressors are on-going and cause long-term environmental problems that can cause catastrophic changes in biodiversity and functioning (Kennish 2002).

Sedimentation is an important process occurring within estuaries that supplies nutrients, buries contaminated sediment, and buffers against coastal erosion

(Thrush et al. 2004). Sedimentation rates are naturally high in New Zealand estuaries and other Pacific Rim countries because catchments have easily erodible sediment, steep terrain, and moderate to low annual freshwater discharge (Milliman and Meade 1983). However, exacerbated inputs of terrestrial sediment, caused by large scale anthropogenic activities (i.e. urbanisation, deforestation, agricultural practices) in catchments, are increasing the vulnerability of estuaries to degradative changes (Thrush et al. 2003; Lohrer et al. 2004). For example, a recent study in the highlands of Sri Lanka found that the rate of sediment runoff increased by two orders of magnitude per year, due to the conversion of forested to agricultural land (Hewawasam et al. 2003). When sediment laden runoff meets seawater, fine particles flocculate and are rapidly deposited on the sediment surface (Ellis et al. 2002; Norkko et al. 2002; Thrush et al. 2004). Over time, terrigenous sediment is gradually incorporated into ambient sediments via mixing, and acquires a marine signature, I term this ‘aged terrigenous sediment’, here on in referred to as TS (Norkko et al. 2002; Cummings et al. 2003; Lohrer et al. 2004).

TS is often composed of fine sediment particles and modifies the physical and biological characteristics of estuaries (Norkko et al. 2002; Lohrer et al. 2004). TS caps the sediment and clogs pore spaces, reducing sediment permeability and decreasing hydraulic conductivity. Changes in these sediment characteristics reduce solute exchange between the sediment and the overlying water column, which modifies geochemical gradients and can induce anoxia. If chronic TS is retained in an area, it may cause long-term habitat degradation compared to a one off disturbance event that sees a lot of material deposited rapidly following storm events. The effect and recovery from TS depends on the magnitude and its persistence through time (Norkko et al. 2002; Lohrer et al. 2004; Romero 2004). There has been extensive work looking at the effects of, and recovery from, catastrophic sedimentation events (2-10 cm thick layer of sediment) (e.g. Peterson 1985; Cummings et al. 2003; Hewitt et al. 2003; Thrush et al. 2003). Such events are episodic and restricted to local zones. When they occur they can smother important vegetation such as sea grass beds (Campbell and McKenzie 2004) and cause mass mortality of macrofauna and, recovery can be extremely slow (Milliman and Meade 1983; Norkko et al. 2002; Cummings et al. 2003; Thrush et al. 2004). Norkko et al. (2002) found that following a catastrophic sedimentation

event, once TS had been dispersed and broken down, surficial sediments were rapidly recolonized by epifauna. However, infaunal communities did not recover during the 408 days of experimental monitoring, which suggests that communities may take years to return to a pre-disturbance state and in many cases post-disturbance communities may be substantially different (Norkko et al. 2002). Thrush et al. (2003) also reported that the smothering of infauna notably affected recovery suggesting that they play a key role in ecosystem functioning.

Unlike catastrophic events which cause mass mortality, the deposition of thinner layers of TS is on-going and more extensive. The effects of smaller (<1 cm layers) but more frequent depositional events have received less attention. Research shows that even thin deposits of TS reduces species richness and the density of common fauna and results in decreased rates of benthic primary production (Lohrer et al. 2004; Rodil et al. 2011).

A low level of TS input may not have a lethal impact (i.e. what happens with catastrophic events) but may alter behaviour causing changes in function (Miller et al. 1992; Woodin et al. 2012). TS is largely composed of silt/clay particles (<62.5 μm) that are highly charged and enriched in poorer quality organic matter, which has been shown to influence prey selection (Safi et al. 2007) and interfere with bivalve feeding which affects condition (Ellis et al. 2002; Hewitt and Pilditch 2004). Changes in the sedimentary environment can also elicit a change in functional role of estuarine organisms, for example, Tellinid bivalves in the *Macoma* genus are known to show a range of feeding modes depending on the environmental conditions (Lopez and Levinton 1987; Levinton and DeWitt 1989; Levinton 1991). *Macoma balthica* modify their feeding mode in response to food availability and quality (Olafsson 1986). Likewise, the behaviour and activity of the bioturbating crab, *Austrohelice crassa*, changes in response to sediment type from a burrow builder in muddy cohesive sediment to a bulldozer in sandier sediments (Needham et al. 2010). Such changes may modify the functionality of benthic communities, affecting benthic-pelagic coupling and ultimately ecosystem functioning. The gross primary productivity of muddy sediment has been measured to be up to 3-4 times lower than in sandy sediments (Jones et al. 2011). Thus, the “muddying” of estuaries is likely to reduce primary productivity which will affect estuarine goods and services.

1.1.2 Macrofaunal influences on benthic-pelagic coupling

Bio-geochemical pathways play a crucial role in benthic-pelagic coupling (Kristensen and Blackburn 1987), and are mediated by macrobenthic communities. The interaction between macrofauna and these pathways increases the rate of organic matter decomposition and nutrient recycling (eg Gray 1997; Herman et al. 1999; Levin et al. 2001), especially when physical disturbance is low (Marinelli and Williams 2003; Kristensen and Kostka 2005; Meysman et al. 2006). Thus if the biodiversity of benthic communities change then so too will benthic-pelagic coupling and ecosystem functioning.

Bioturbating macrofauna are ecosystem engineers (sensu Jones et al. 1994) who through their activity, alter grain size distribution, chemical and pressure gradients and also influence habitat structure and resource availability (eg Lohrer et al. 2005). Bioturbation is the displacement of particles due to biological activity (feeding, excretion and movement) (Boudreau 1998; Meysman et al. 2006). Bioturbators play an important role in the exchange of particles across the sediment-water interface by destabilising sediment increasing its erodability (Lelieveld et al. 2004) and increasing the surface area for solute exchange between the porewater and the overlying water column (benthic-pelagic coupling) (Lohrer et al. 2005). The exchange of solutes is important as it drives the oxygen dynamics within the sediment, which cause changes in the geochemical condition, microbial diversity, rates of microbial processes, the size of the inorganic and organic pools and their respective changes within a sediment body (Rocha 2008).

Solute transport in sediments may be via molecular diffusion or advective transport. Molecular diffusion is the slow diffusion of molecules from an area of high concentration to low concentration (Forster et al. 1996). It is the main mode of solute transport in muddy cohesive sediments where permeability is low, because the pressures required to force porewater flow through sediments are generally greater than the physical processes or macrofauna are capable of generating (Forster et al. 1996; Glud et al. 1996). Advective transport becomes important in permeable sandy sediments; it occurs in response to pressure differences at the sediment-water interface and is a much faster mode of solute transport (Glud et al. 1996). Pressure gradients are generated by both physical and biological processes (Forster et al. 1996; Huettel et al. 1996; Ziebis et al. 1996;

Pilditch et al. 1997). For example, the physical interaction of boundary currents with topography creates areas of high and low pressure (Precht and Huettel 2003) and wave induced oscillatory flows enhance pressure differences with the passing of wave troughs and crests (Precht and Huettel 2004). Infaunal species that live freely in the sediment create pressure gradients and drive porewater flows that penetrate surrounding sediments via bioadvection (Marinelli 1992; Meysman et al. 2005; Waldbusser and Marinelli 2006).

Bioadvection is the movement of interstitial water through the sediment in response to changes in the local pressure field created by the hydraulic activity (burrowing, feeding, and defecation) of infauna (Volkenborn et al. 2010). Unlike bioturbation, which enhances the transport of sediment particles, bioadvection enhances the transport of solutes and can also induce the movement of particles (Glud 2008). Through their hydraulic activities, infauna change interstitial pore pressure and induce porewater flow in the direction of the pressure gradient. For example, when *Arenicola marina* feeds it sucks water into the sediment, thereby increasing interstitial pressures, and driving an efflux of nutrient rich, oxygen depleted porewater into the overlying water column. Whereas, when *Arenicola marina* defecates it decreases interstitial pressure, driving an influx of oxygen-rich water from the water column into the sediment (Volkenborn et al. 2007; Wethey et al. 2008; Woodin and Wethey 2009; Volkenborn et al. 2010). The scale of this effect is dependent on several factors, including sediment type, organism size, depth of burial and the hydraulic conductivity of the sediment (which is a function of the porosity and permeability) (Marinelli and Williams 2003; Volkenborn et al. 2010). In permeable sediment, bioadvective flows can affect porewater at depths of 10-20 cm, as well as at the surface (Wethey and Woodin 2005; Wethey et al. 2008; Volkenborn et al. 2010; Woodin et al. 2010).

Macomona liliana (Tellinid bivalve) are commonly found in intertidal soft sediment habitats of New Zealand and are often numerically and biomass dominant (Hewitt et al. 1996; Lundquist et al. 2004; Cummings et al. 2009). They are ecosystem engineers who alter habitats and influence the resources available to other organisms through their feeding and activity (Jones et al. 1994; Volkenborn et al. 2007). *M. liliana* live at depths of up to 10 cm below the sediment (Thrush et al. 1996), but this varies with organism size and sediment

type (*pers. obs.*). *M. liliana* generate bioadvective flows and their feeding has been shown to be important in driving sediment oxygen dynamics. *M. liliana* are deposit feeders that have two separate mobile siphons: an inhalant and an exhalant. Their inhalant siphon is used to collect particles beneath, on and just above the sediment surface. A strong inhalant current is generated in the siphon by the lateral cilia of the ctenidium (Ward and Shumway 2004). This draws oxygen rich water, laden with particulate matter, into the frontal surfaces of the ctenidium, which is adapted to handling large masses of material. Particles are then transferred to the palp, and sorted (pre-ingestion sorting), some are rejected as pseudofaeces through the exhalant siphon and others are transferred to the gut. Once in the gut, particles are again sorted (post-ingestion sorting); organic matter is absorbed in the digestive gland and inorganic matter is rejected as faeces through the exhalant siphon (Ward and Shumway 2004). The exhalant siphon generally sits below the sediment surface, and pseudofaeces, faeces and filtered water is injected into the sediment, rather than the overlying water column. This creates a column of faecal pellets, within the vicinity of the exhalant siphon, which extends to the sediment surface. The plume of water oxygenates a pocket of surrounding sediment and pressurises the sediment, driving bioadvective porewater flows (Volkenborn et al. under review).

Oxygen dynamics within sediments have been directly related to porewater pressurisations created by feeding in three Tellinacean bivalves (*Macoma balthica*, *Macoma nasuta* and *Macomona liliana*). During sediment pressurisation, an oxic pocket was formed at the injection point and these collapsed completely as oxygen was consumed by the sediment during non-pressurised periods (Volkenborn et al. under review). This suggests that the interplay between the hydraulic activity of infauna and sedimentary oxygen consumption rates drive oscillatory geochemical conditions up to six times per hour (Volkenborn et al. under review). Oscillatory conditions observed on the scale of hours to days as a result of burrow irrigation (Caradec et al. 2004), have been shown to drive higher rates of nutrient recycling due to different microbial assemblages being activated during oxic and anoxic conditions. Therefore, sediments with oscillating geochemical conditions support higher primary productivity than sediments with stable redox conditions (Sun et al. 1993; Aller 1994; Sun et al. 2002; Cravo-Laureau et al. 2011; Bennett et al. 2012). The oscillations in the geochemical

conditions caused by *M. liliana* feeding are on much shorter time scales (minutes compared to hours) and therefore are likely to contribute to faster nutrient recycling. Changes in feeding behaviour may affect geochemical oscillations, which will have important implications for nutrient recycling and estuarine productivity.

M. liliana are sensitive to small TS deposits, including abundance declines (Lohrer et al. 2004), reduced juvenile burial rates (Cummings and Thrush 2004; Cummings et al. 2009) and increased behaviours associated with emigration and relocation of feeding zones (Woodin et al. 2012). Many species of Tellinid bivalves are primarily deposit-feeders however, they show functional plasticity in feeding mode, switching between deposit-feeding and suspension-feeding, in response to changes in environmental conditions, food availability and predation (Levinton 1991). *M. liliana* may also show changes in feeding mode and associated behaviours in response to TS. Deposit-feeding and suspension-feeding are functionally different; deposit-feeding bioturbates the sediment surface whereas suspension-feeding does not. A change in feeding mode may cause changes in the functionality of the community. Additionally, *M. liliana* have been shown to be hydraulically active up to 94% of the time (Volkenborn et al. under review) and therefore, changes in behaviour are likely to modify solute transport and influence geochemical gradients, which over time could affect ecosystem functioning.

The aim of this study was to gain a mechanistic understanding of how *M. liliana* behaviour changes in response to TS and infer how these changes may potentially affect porewater fluxes. This is important because the hydraulic activities of infauna drive porewater flow through bioadvection, which influences benthic-pelagic coupling and ultimately ecosystem functioning. This research builds on a recent field experiment that demonstrated *M. liliana* behaviour changed with the addition of thin TS, where there was an increase in behaviours associated with finding more favourable sediment conditions (Woodin et al. 2012). However, due to environmental, logistical and equipment restraints, replication in Woodin et al. (2012) was low and may not have accounted for the natural variability of *M. liliana* behaviour. In the experiment, behaviours in the field were classified by pressure signals associated with certain behaviours, which were pre-determined by cross referencing surface images of *M. liliana* with

pressure signals recorded within the sediment. However, the *M. liliانا* used to determine behaviour were not exposed to TS and were not the same as those in the experiment therefore, variability in signals produced by individuals may have affected results.

1.2 Objectives and Hypotheses

This is the first laboratory based experiment looking at the effects of TS on the infaunal bivalve behaviour, and linking these to potential changes in porewater flux. The experiment focussed on the effect of small amounts of TS (<1 cm thick). It has been shown that catastrophic sedimentation events cause mass mortality of benthic macrofauna, affecting ecosystem functionality. I wanted to determine whether small deposits of TS, which are widespread and occur regularly, affect ecosystem functioning by causing changes in the behaviour of a dominant member of benthic community.

The objective of this project was to investigate the effect of thin TS on *M. liliانا* behaviour and infer potential implications for porewater fluxes, ultimately affecting ecosystem functioning. *M. liliانا* behaviour was classified and quantified at the sediment surface by time-lapsed images and sub-surface by pressure sensors. To simulate natural occurrences of TS, three treatments (high, low and mixed; Table 1) were tested. These were within ambient ranges that *M. liliانا* are exposed to and caused only minor changes in the sediment properties (Hewitt et al. 1996). By conducting laboratory experiments I was able to simultaneously record surface and sub-surface activity of *M. liliانا* and this provided a concise look at how their bioturbating and hydraulic behaviours were modified by small amounts of TS. Additionally, I was able to increase replication compared to replication in Woodin et al. (2012) and manipulate the sedimentary environment, whilst controlling for other confounding variables.

A priori predictions:

1. The addition of small amounts of TS would alter the characteristics of the surface sediment, by decreasing hydraulic conductivity, as well as increasing the silt/clay and organic matter content. In addition, it was expected that these changes would be more pronounced with increasing TS.

2. That behavioural response of *M. liliana* would be subtle, as only small amounts of TS were added and these responses would vary with the magnitude of the treatment.
3. Increases in activities associated with searching for better conditions (movement and siphon relocation), as these had previously been observed (e.g. Woodin et al. 2012).
4. Behaviour associated with feeding (defecation, the mode and time allocated to feeding) would change with the addition of TS, which has been shown to change the quality of food and affect bivalve feeding (Taghon and Jumars 1984; Jumars and Wheatcroft 1989; Ellis et al. 2002; Safi et al. 2007).
5. That changes in *M. liliana* behaviour would cause changes in sediment pressurisation. Furthermore, changes in the sediment properties may alter porewater flux.

CHAPTER TWO: MATERIALS AND METHODS

The aim was to investigate the effect of thin TS (aged terrigenous sediment) deposits on *M. liliana* behaviour and relate these to potential changes in porewater fluxes. Surface behaviour of *M. liliana* was measured using time-lapse imagery and sub-surface behaviour using high frequency pressure sensors buried in the sediment.

2.1 Experimental treatments and set up

A series of mesocosm experiments were conducted under continuous flow to investigate the effect of TS on the behaviour of *M. liliana*. Experiments were conducted in a recirculating flume tank, described in Miller et al (2002), to mimic ambient flow conditions. The flume was an acrylic channel (723 cm x 50 cm 50 cm) with a 40 cm diameter return pipe running beneath the flume with an impeller in the descending arm of the return pipe to regulate flow speed. A working area was located 500 cm downstream of the entrance point, where an insert was fitted that allowed eight mesocosms (13 cm diameter, 15 cm deep) (Figure 2). Each mesocosm contained one *M. liliana* and one pressure sensor. A camera was set up 25 cm above each pair of mesocosms to capture images of the sediment surface (Figure 3c). To simulate the on-going addition of small amounts of TS in estuaries three TS treatments were chosen. When TS is deposited on the sediment surface it accumulates and either remains as a layer on the surface or is worked into ambient sediment through physical and biological processes. To simulate this in the laboratory low (L), mixed (Mx) and high (H) sediment treatments (Table 1) were chosen, which in preliminary tests, had a significant effect on hydraulic conductivity. A control with no TS added was used to determine whether changes in behaviour were due to TS addition or a function of time. Each treatment was duplicated in a single experimental run and the experiment was repeated five times. Experiments ran for 60 h with data collection for 32 h pre-treatment, a 4 h interval during treatment addition and 24 h of post-treatment data collection.

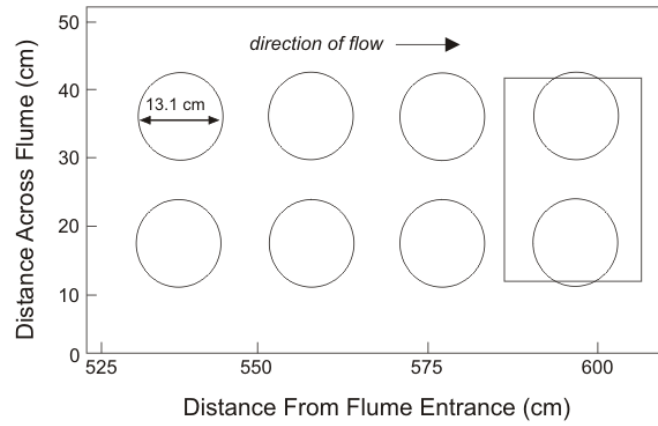


Figure 2: Plan view of the flume insert showing experimental layout, the mesocosms are the eight evenly spaced circles and the rectangle indicates the area covered a single camera.

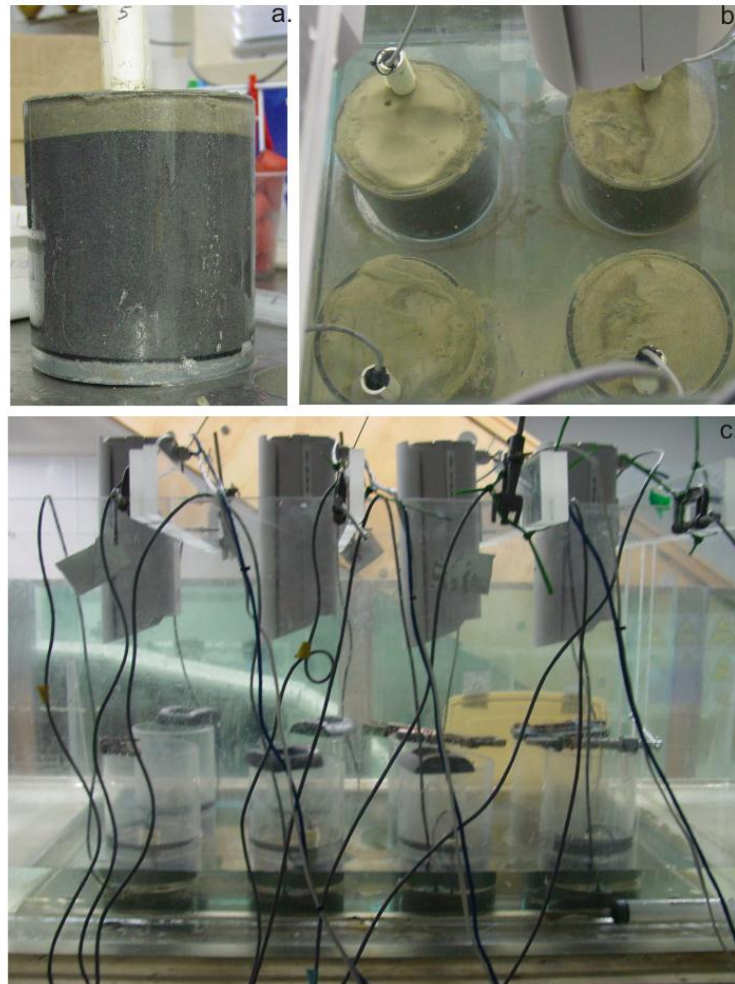


Figure 3: Experimental set-up; (a) sediment structure of a mesocosm with a deployed pressure sensor, (b) post-treatment addition; clockwise from top left to bottom right treatments are low, mixed, high and mixed, (c) cameras set-up over mesocosms during treatment addition.

2.2 Experimental protocol

Sediment for the mesocosms and *M. liliانا* specimens (sized 30-40 mm) were collected from a clean sandy site (37°01.0255S, 174°49.0767E) on Wairoa Island, which is located in the eastern part of the Manukau Harbour, on the west coast of the North Island, New Zealand. Wairoa Island has extensive shallow intertidal sandflats that are approximately 1.8 km wide (Thrush et al. 1997), with a community dominated by *Austrovenus stutchburyi* and *M. liliانا* (Cassie and Michael 1968; Pridmore et al. 1990). Sediments at this site were predominantly comprised of well sorted fine sands with a small proportion of mud and shell hash (Dolphin et al. 1995; Bell et al. 1997). There was a distinct oxic layer, (indicated by colouration differences), approximately 2 cm deep at the collection site and for this reason ambient oxic and anoxic (2-10 cm) sediment was separated during collection. Sediment was sieved on site across a 1 mm mesh to remove large macrofauna that would introduce noise to the pressure records. Additional cores (5 cm diameter, 10 cm depth) were collected for hydraulic conductivity measurements. TS for the treatments was collected 150 m up-stream near the Pukaki channel (37°01.0243S, 174°49.0777E) and was sieved through a 63 µm mesh to isolate the silt/clay fraction resulting in TS with an average grain size of 31 µm. To minimise variability in sediment characteristics, sediment for all the experiments was collected on one day and stored in a freezer. To avoid stress to *M. liliانا*, organisms were collected on the day of each experimental run and transported back to the laboratory in a cool, aerated chilli bin filled with sea water from the site. Bivalves were then placed in an aerated aquarium with running seawater until the experiment commenced.

To measure changes in sub-surface behaviour, a pressure sensor (30 kPa, stainless steel membrane, referenced in watertight housing, Measurement Specialties Inc.) was buried 10 cm deep into each mesocosm. These sensors measured changes in pressure by determining the difference in hydrostatic pressure measured at a sub-surface and reference port and are capable of high frequency sampling. The sub-surface port protruded through the wall of the pipe and was covered with 64 µm nylon mesh to prevent damage to the sensor membrane. The reference port was in a common seawater plenum on the inside of the pipe, the top of the plenum was 6-8 cm above the sediment surface (Figure 3a),

allowing the reference ports of the sensors to be exposed to the hydrostatic pressure of the overlying seawater. Porewater pressure was recorded at 200 Hz, using an autonomous data logger (Persistor Instruments, Bourne Massachusetts, USA) (Wetthey and Woodin, 2005). The pressure sensors have been shown to detect the hydraulic pressure signals of *M. liliana*, laterally, tens of centimetres away from an individual (Woodin et al. 2010). Given this information, the sensors were placed to the side of the mesocosms to minimise the interference with flow and *M. liliana* activity. Prior to each deployment the pressure sensors were calibrated by immersion and emersion in known water depths from 0-20 cm ($r^2 > 0.9$) in saltwater to be used in the experimental runs (see Volkenborn et al. 2010).

To replicate ambient conditions sediment was added to mesocosms in two layers (oxic and anoxic) (Figure 3a). Sediment was added around the pressure sensor using the method described in Volkenborn et al. (2010) to avoid air pockets and compaction. Mesocosms were placed in an aquarium with an air stone and running seawater for 48 h to re-establish ambient porosity and chemical gradients (Wetthey et al. 2008; Woodin and Wetthey 2009; Volkenborn et al. 2010). After 48 h, the mesocosms were placed in the flume so that the sediment surface sat flush with the insert. The flume was then filled with seawater to a depth of 19 cm and flow was turned on. The salinity and temperature were measured to ensure they were within ambient ranges, at the time of sampling, ($S = 30\text{--}32$ PSU and $T = 15\text{--}17$ °C). To prevent movement of the TS, a flow speed below the erosion threshold was chosen (10 cm s^{-1} ; pers.obs.). To measure surface behaviour of *M. liliana*, a high resolution camera was set up over pairs of mesocosms (Figure 2 & 3c). The cameras were capable of time-lapsed imagery and captured an image of the sediment surface every 10 s. The cameras and pressure sensors were time-synchronised to allow comparison. At this point, data collection by the cameras and pressure sensors was initiated, *M. liliana* were randomly allocated to each of the mesocosms, placed on the sediment surface and allowed to bury. Data was collected for 36 h under these conditions to capture “pre-treatment” behaviour. After 36 h the flow in the flume tank was stopped and the TS treatments (Table 1) were randomly allocated to each of the mesocosms.

Table 1: Treatment information; dry weight of TS added per cm² and layer thickness (mm).

Addition	Sediment added dry weight (g cm ⁻²)	Approximate thickness on sediment surface (mm)
Control	0.00	0
Low	0.09	1
Mixed	0.20	Mixed through top 2 cm of sediment
High	0.20	4

For the addition of the treatments the water level was lowered. The mixed layer treatment was added first, by siphoning off the oxic layer and adding a TS and oxic sediment mixture. The low and high treatments were added as TS slurries through core barrels that fitted over the mesocosms. The core barrel formed a seal with the insert, allowing the sediment to settle out naturally through the water column without it influencing other treatments. Core barrels were also placed over the control and mixed treatments to prevent any drift of TS onto the sediment surface. After four hours the majority of silt/clay had settled, at which point the core barrels from the low and high treatments were removed and the flow was turned on to 2 cm s⁻¹, so that any sediment still in suspension would be swept away from the other treatments. After 10 min the flow was increased to 10 cm s⁻¹ and the core barrels from all other mesocosms were removed. The water level was then raised back to 19 cm. Data collection continued for a further 24 h post treatment addition (covering the period of two tidal cycles), after which the experiment was broken down.

At the end of each experiment, sediment cores (2.5 cm diameter, 2 cm deep) from each of the mesocosms were collected and frozen to determine sediment characteristics (grain size, organics and Chlorophyll *a*). Sediment samples for grain size analysis were digested in 10% hydrogen peroxide, to remove organic matter (Day 1965) before analysis on a Malvern Mastersizer 2000. The organic content of samples was determined by the loss on ignition method described by Ball (1964). Chlorophyll *a* and phaeopigments (phaeo) (extraction in 90% acetone for 20 h at 4 °C in darkness) was determined using 10-AU Turner design Flurometer (Parsons et al., 1984). A constant head method described in Klute and Dirksen

(1986) was used to determine the hydraulic conductivity of saturated ambient, control and treatment sediment cores (5 cm diameter, 10 cm length).

Burial is commonly used as an indicator of organism health (Cummings and Thrush 2004). After each experiment re-burial tests were run in mesocosms sitting in an aerated aquarium to ensure the experimental process had not caused any detrimental health effects, which may have had a significant effect on *M. liliana* behaviour. The ability of *M. liliana* to bury and the time it took to bury was recorded. Individuals were then frozen for condition analysis which, involved measurements of the shell dimensions (length, width and depth) and dry weight of the flesh and shell as in Roper and Hickey (1994).

2.3 Behaviour classification

Images of the sediment surface were used to create time-lapsed videos, which provided counts of activity at the surface without time stamps. Video footage was quantified 24 h pre- and post-treatment addition with analysis starting 12 h into the 36 h pre-treatment to allow individuals time to acclimatise. Pressure sensors provided sub-surface behavioural counts, as well as information on timing and duration of events. To remove noise, data collected by pressure sensors were run through a custom smoothing program written by David Wethey (University of South Carolina) in the statistical software package R version 2.14. The clean records were then analysed in Matlab version R2011b to determine pre- and post-treatment behaviour (see Appendix 1 for pressure records). Analysis of the records started 10 h after disturbances (introduction of the *M. liliana* to the cores and treatment addition), so that *M. liliana* had time to become established and adopt 'normal' behaviour. Five behaviours similar to those classified in Woodin et al (2012) were identified in the video footage and pressure records; movement, deposit-feeding, suspension-feeding/ventilation, siphon movement and claps (Figure 4). Siphon relocation and inactivity were only classified in the video and pressure records, respectively. Classifications of behaviours based on pressure signals were cross-checked against camera images following Volkenborn et al (2010). Pressure records were analysed at two scales. To classify small scale behavioural patterns (siphon movement, clapping, organism movement, feeding

and inactivity), 8 h of pressure record were analysed at a high resolution for both the pre- and the post-treatment (dashed line Figure 5). So that larger scale behavioural patterns were captured in the analysis, it was extended for a further 8 h (solid line Figure 5) looking at a reduced set of behaviours; organism movement, feeding and inactivity.

Movement

Through their activity *M. liliana* bioturbated surface sediment, modifying the sedimentary environment. When *M. liliana* moved they disturbed the sediment surface causing cracks and upheaval, which in the pressure record created dense up and down signals (Figure 4a & b; Figure 5c).

Siphon movement

M. liliana have two siphons, an inhalant and exhalant, which were observed to be moving around, in and out of the sediment. Siphon movements created sharp positive peaks in the pressure record. Inhalant siphon movements occurred more commonly when the animal was at rest (Figure 5d), whereas exhalant siphon movements occurred during pressurisations (Figure 5c); for data analysis this was grouped as ‘siphon movement’.

Feeding

As well as bioturbating the sediment surface, *M. liliana* feeding caused pressurisation of the pore spaces at depth, creating bioadvective flows. Two feeding behaviours were distinguishable from the video footage and pressure records; deposit-feeding and suspension-feeding/ventilating. Both created positive pressurisations; deposit-feeding produced bursts of short pressurisations (Figure 5d), whereas suspension-feeding/ventilation created longer periods of pressurisation. In the video footage, the two feeding types were clearly distinguishable; deposit-feeding bioturbated the sediment surface leaving tracks (Figure 4d) and suspension-feeding/ventilation had no contact with the sediment surface (Figure 4e & f). Suspension-feeding and ventilating were grouped together because *M. liliana* were essentially functioning the same by inhaling water (confirmed by pressure records); however it could not be determined whether this was for food or for oxygen. In the video, this was seen as the inhalant

siphon sitting in the water column (Figure 4e) or visibly in a feeding/ventilation hole (Figure 4f).

Claps

Clapping was comprised of coughing pseudofaeces production and defecation, all of which produced sharp negative spikes in the pressure record (Figure 4g, h & i), and were associated with feeding and the removal of unwanted material. In Woodin et al (2012) these behaviours were differentiated, however this was difficult to do in the present study due to sediment permeability. Recent research by Volkenborn et al. (under review) showed that these events play a small role in driving porewater fluxes. In light of this information and for the purpose of this study, defecation and coughs were grouped into a collective term ‘claps’ (Figure 5d).

Siphon relocation

Siphon relocation is associated with individuals searching for better conditions. This was seen in the video footage as a new hole opening up in the sediment (Figure 4c). When individuals are at rest/inactive the hydrostatic pressure returned to baseline in the pressure records (Figure 5d).

2.4 Statistical analysis

To account for natural variations in activity, a normalised biometric was calculated for each of the behaviour types; $\Delta F = \frac{(b-a)}{(a+b)}$ where ΔF = frequency change in behaviour, a and b = behaviour count pre- and post-treatment, respectively. A $\Delta F = 0$ indicates no change in behaviour after the treatment addition. A positive or negative ΔF indicates an increase or decrease, respectively, in the frequency of behaviour after treatment addition.

The conditions for each experiment were the same in every run and it was assumed that the treatment duplicates were independent of one another and therefore were treated as replicates for statistical analyses. Statistical analyses were carried out in STATISTICA and data were checked for normality and homogeneity of variance. In cases where the assumptions of the data did not hold true data were log transformed. Differences in sediment characteristics between

treatments were determined using one-way Analysis of Variance (ANOVA). Significant results were further analysed using a post-hoc Newman-Keuls test. Significant changes in behaviour were determined by testing ΔF against zero using a single sample t-test or one-way ANOVA to compare between treatments for raw measurements of event durations and height of pressurisations.

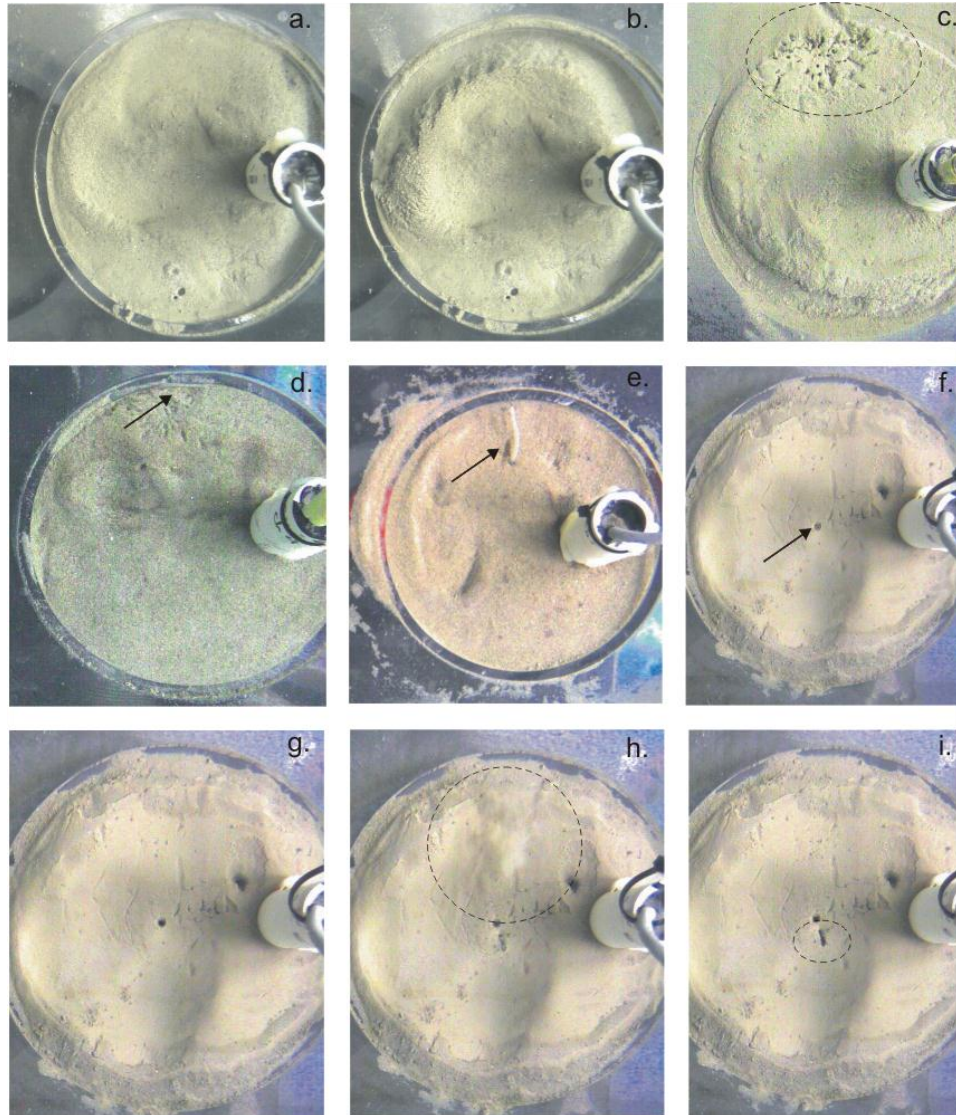


Figure 4: Examples of *M. liliana* behaviours observed in the video footage; sediment surface (a) before (b) and after a movement event, (c) sediment reworking caused by siphon relocation and deposit-feeding (circled), (d) inhalant siphon deposit-feeding, (e) inhalant siphon sitting in the water column suspension-feeding/ventilating, (f) inhalant siphon sitting in the feeding hole suspension-feeding/ventilating, sequence showing coughing, (g) before cough (h) mid cough with sediment plume (circled) and (i) a new hole made after cough (circled). Arrows point to inhalant siphon.

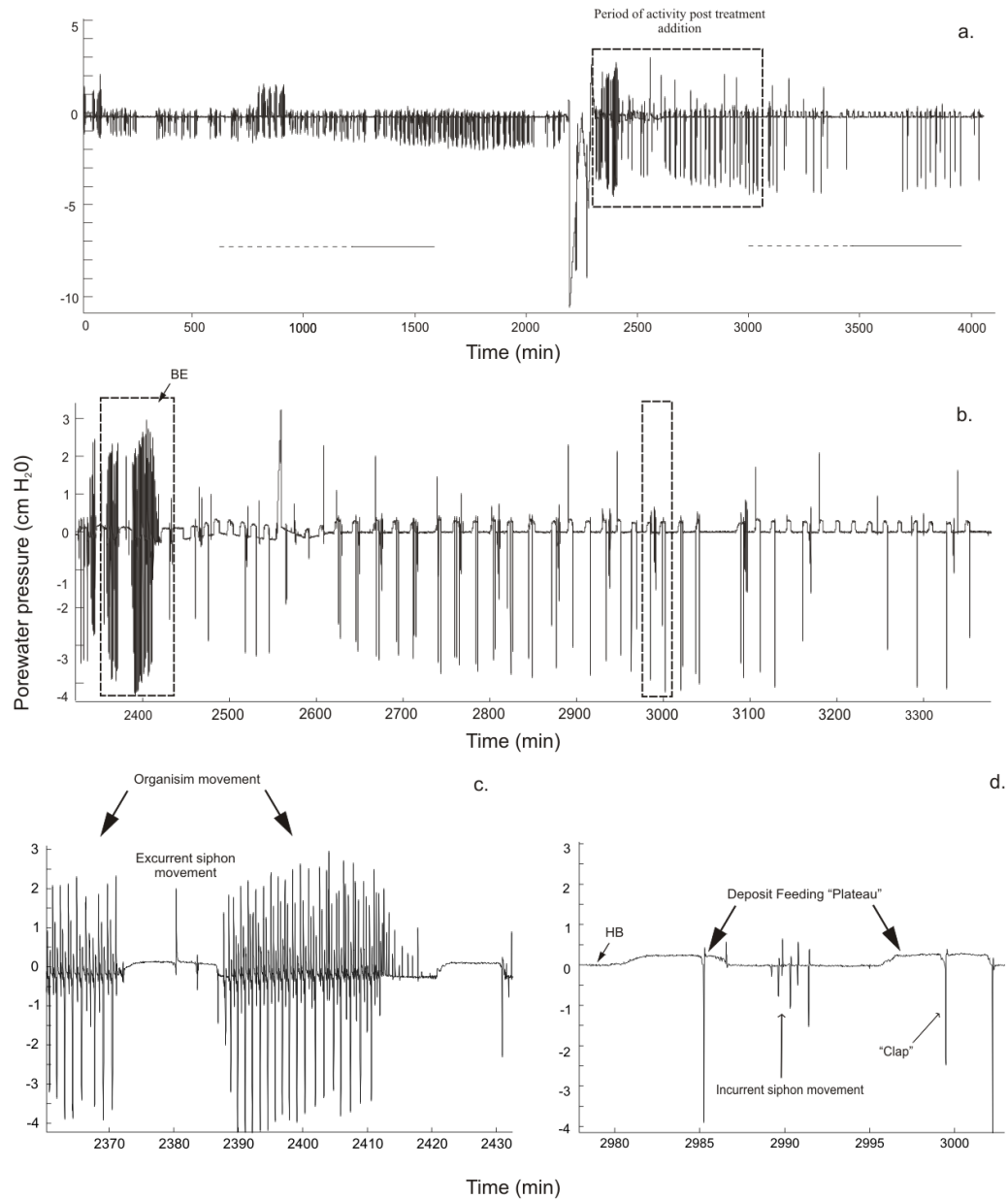


Figure 5: Porewater pressure dynamics associated with hydraulic activities of *M. liliana*. (a) Shows a 67 hour sequence starting with burrowing episodes (BE) after which the individual begins to deposit-feeding, characterized by intermittent pressurisation and return to hydrostatic base line (HB), positive and negative hydraulic pulses associated siphon movements and claps, respectively. The lines below the pressure signals indicates the segment analysed, the dashed line was analysed in depth while the solid line was analysed only for large scale activities. (b) An enlargement of the pressure data as indicated by the dashed box in (a). (c) & (d) Enlargements of the pressure data as indicated by the dashed boxes in (b).

CHAPTER THREE: RESULTS

3.1 Sediment parameters

How effective the treatments were at changing the sedimentary environment was determined by hydraulic conductivity measurements for all treatments and analysis of sediment surface samples taken after each experiment. Sediment properties varied significantly among treatments (Table 2). One-way ANOVA and Newman-Keuls post-hoc tests found the silt/clay and organic content increased with TS addition, whereas hydraulic conductivity decreased. The hydraulic conductivity of the mixed treatment was an order of magnitude lower than the other three treatments despite having the same silt/clay content as the high treatment. Sediment Chlorophyll *a* was significantly lower in the mixed treatment compared to all other treatments, which showed no significant differences. Sediment characteristics of the control were similar to those measured at the collection site. Although on average, the control had higher chlorophyll *a* concentrations (25 %) and organic content (0.35 %).

Table 2: Sediment parameters of experimental treatments; hydraulic conductivity (K), silt/clay content, Chlorophyll a content (Chl a) and organic content, one-way ANOVA p and results of Newman-Keuls post-hoc tests (C= control, L= low, Mx= mixed and H =high).

Variable	Treatment Mean \pm SE				n	p	Post hoc
	Control	Low	Mixed	High			
K (cm s ⁻¹)	$9.0 \pm 0.4 \times 10^{-3}$	$6.0 \pm 0.9 \times 10^{-3}$	$0.9 \pm 0.2 \times 10^{-4}$	$2.0 \pm 0.5 \times 10^{-3}$	19	0.000	C = L > H > Mx
Silt/Clay (%)	0	1.6 ± 0.5	6.5 ± 0.6	6.1 ± 0.8	38	0.000	C < L < Mx = H
Chl a ($\mu\text{g g}^{-1}$)	16.0 ± 0.3	15.8 ± 0.7	13.1 ± 1.1	16.1 ± 0.4	40	0.006	Mx < C = L = H
Organic content (%)	0.36 ± 0.01	0.48 ± 0.01	0.63 ± 0.01	0.62 ± 0.03	40	0.000	C < L < Mx = H

3.2 Behavioural analysis

To determine if TS causes behavioural changes in *M. liliana*, behaviour was analysed before and after treatment additions. Cameras were positioned over mesocosms to capture footage of surface behaviour. Sub-surface behaviour was captured by pressure sensors buried in the sediment. The two methods of data collection were synchronised so that they were complementary and could be used to cross reference behaviour classifications. For each treatment, there were a total of ten replicates, however not all were viable due to equipment failures. The number of usable replicates is given in Table 3.

3.2.1 *Macomona liliana* condition

M. liliana were collected fresh for each run on the day that data collection was initiated. To determine whether the initial health of *M. liliana* changed over the duration of the experiment, pre-treatment burial rates were timed. A significant difference in burial rates was found (one-way ANOVA, $p = 0.01$), where burial rates in the second and third experiment were significantly faster than those recorded in the fourth and fifth experiment (9, 8, 17, 16 min, respectively) (burial tests were not run in the first experiment). However, there was no significant difference in the condition of individuals used between experiments (one-way ANOVA $p = 0.88$) and it was therefore assumed all *M. liliana* were of the same health. To determine whether the treatments had any short-term effect on health, post-treatment burial tests were conducted. Pre- and post-treatment burial rates were compared in a paired t-test for each treatment and no treatment effect on burial was found (one-way ANOVA $p = 0.36$) (Figure 6).

Table 3: Number of treatment replicates for each observation method.

Treatment	Video	Pressure Sensors
Control	9	6
Low	9	10
Mixed	8	9
High	10	7

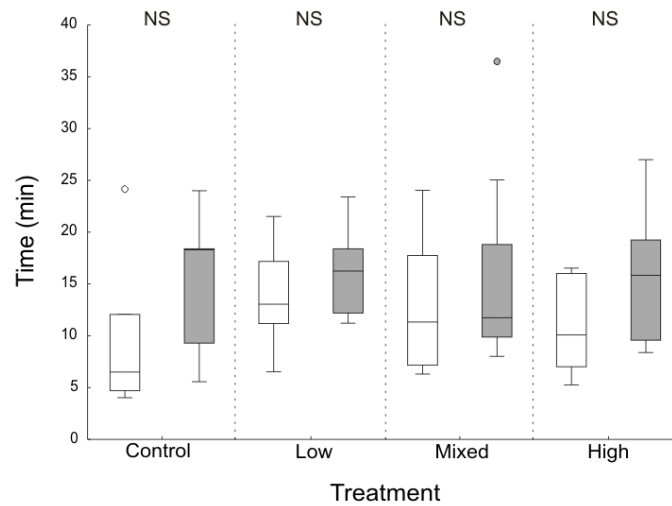


Figure 6: Burial rates pre- (white boxes) and post- (grey boxes) treatment addition. The solid horizontal line is the median, the box represents the 25th and 75th percentiles, the whiskers are the non-outlier range and the circles represent outliers. One-way ANOVA non-significant results are reported as NS.

3.2.2 Video analysis

Video footage provided counts of behaviour visible at the sediment surface (movement, deposit-feeding, suspension-feeding/ventilation, clapping, siphon movement and siphon relocation). Single sample t-test of the surface activities of *M. liliana* revealed that there was no significant difference in ΔF for any behaviour in the control, but there were significant differences in TS treatments. The low treatment showed significant differences in suspension-feeding/ventilation (Figure 7c, Table 4) and siphon movement. In addition to these behaviours, the mixed treatment also showed a significant difference in siphon relocation. The high treatment showed the strongest response to TS with significant differences in all behaviours except deposit-feeding (Figure 7c, d, e & f, Table 4). Additionally, there was a decrease in the variability of response in most of the behaviours for the TS treatments when compared to the control. In the video footage, *M. liliana* movement disturbed up to 50% of surface sediment (Figure 4a & b). There was no significant difference in *M. liliana* movement pre- and post-treatment additions (Figure 7a). Changes in the number of movement events became more variable as TS increased, with the mixed treatment showing the greatest variability (coefficient of variance (COV) = 618).

M. liliana are deposit feeders that feed on organic matter at the sediment surface through an inhalant siphon. The addition of TS modified the properties of surface sediment (Table 2) and this could potentially cause a change in deposit-feeding behaviour. No significant difference was found in deposit-feeding pre- and post-treatment addition (Figure 7b). However, the frequency of deposit-feeding decreased in the majority of individuals in the low treatment, with a median of 20% fewer deposit-feeding events. In the high treatment, there was a cluster of individuals that showed an increase in deposit-feeding ranging from 10-50% and the median was skewed by a few individuals that showed a decrease in deposit-feeding (Figure 7b). In the mixed treatments, changes in deposit-feeding behaviour were highly variable (COV = 345) with clusters around zero, 1 and -1. In contrast, the number of suspension-feeding/ventilating events increased after treatment additions. The strength of the response increased from the control to the high treatment and variability decreased $C < L < H < Mx$ (COV = 263, 141, 90, 51 respectively) (Figure 7c).

Although clapping plays a small importance in driving porewater fluxes (Volkenborn et al. under review) changes in these behaviours may affect the bioenergetics of individuals which could, in the long-term, affect population dynamics and subsequently ecosystem functioning. Behavioural counts showed a significant decrease in the high treatment (Figure 7d) and no significant difference in the low and mixed treatments, but the data may have been skewed by individuals that showed an increase in clapping. Siphon movement and siphon relocation are associated with finding more favourable conditions. Siphon movement increased significantly for all treatments other than the control, which was skewed by individuals showing a decrease in siphon movement (Figure 7e). The variability was greatly reduced in the high treatment compared to the other TS treatments; $C < L < Mx < H$ (COV = 211, 118, 116, 46, respectively). The frequency of siphon relocation decreased significantly in the mixed and high treatment. A significant difference was not found in the low treatment, due to increased siphon relocation by a single individual skewing the data, however there was a trend of increasing response strength with increasing TS, $C > L > H > Mx$ (Figure: 7d & Table 4).

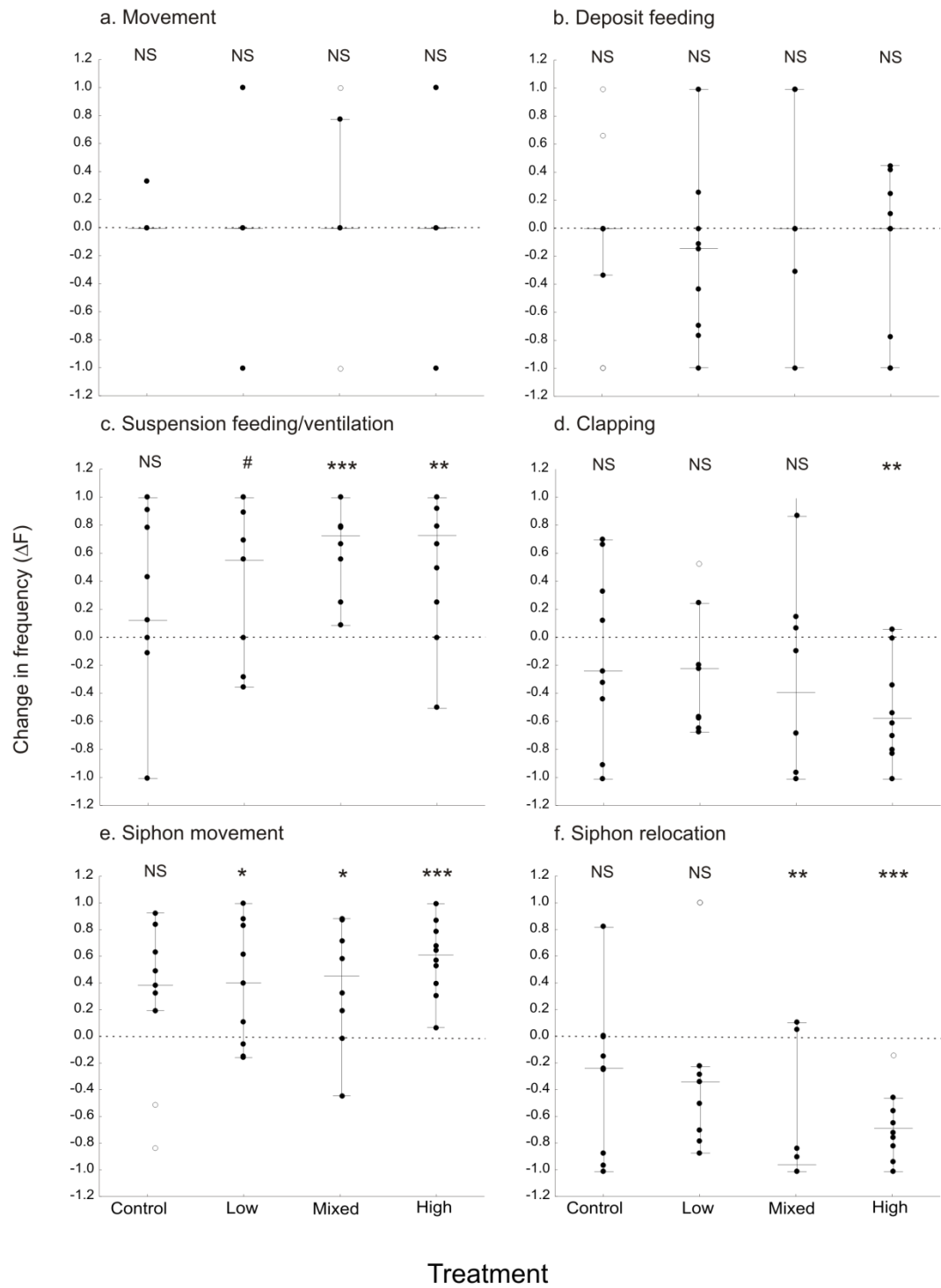


Figure 7: ΔF values for behaviours observed in the video footage. The black dots are the raw data, the solid horizontal line is the median, the whiskers are the non-outlier range and the circles represent outliers. The dashed line highlights no behaviour change pre-/post- treatment; a positive or negative value shows respectively an increase or decrease in behaviour after the treatment additions. Single sample t-test results are reported as; NS = non-significant, # = $0.1 < p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Table 4: Treatment averages (\pm 1SE) from video footage for movement (M), deposit-feeding (DF), suspension-feeding/ventilation (S/V), claps (C), siphon movement (SM) and siphon relocation (SR). See Figure 7 for ΔF values.

Behaviour	Treatment Mean \pm SE							
	Control		Low		Mixed		High	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
M	0	0	0	0	0	1 \pm 1	0	0
DF	2 \pm 1	1 \pm 1	3 \pm 2	4 \pm 2	6 \pm 3	3 \pm 2	10 \pm 4	5 \pm 2
S/V	5 \pm 2	9 \pm 3	12 \pm 7	13 \pm 3	12 \pm 5	23 \pm 6	3 \pm 1	17 \pm 5
C	16 \pm 5	12 \pm 5	11 \pm 2	7 \pm 2	13 \pm 5	6 \pm 3	14 \pm 3	5 \pm 1
SM	13 \pm 4	29 \pm 10	30 \pm 13	45 \pm 11	28 \pm 9	55 \pm 16	18 \pm 9	72 \pm 20
SR	24 \pm 6	10 \pm 4	20 \pm 6	9 \pm 3	22 \pm 5	7 \pm 3	12 \pm 5	9 \pm 4

3.2.3 Pressure sensor analysis

There were fewer viable replicates from the pressure sensors compared to video footage in most treatments, due to sensor malfunctioning (Table 3), which reduced the strength of statistical analysis. However, the time series from the pressure sensors provided valuable information on counts and time allocated to sub-surface behaviour of *M. liliana*, as well as behaviours not easily or reliably quantifiable from the surface.

Organisms often shut down and wait for more favourable conditions when under stress, *M. liliana* did not respond this way to TS. In contrast, after treatment addition there was an increase, although not significant, in the average time spent active (one-way ANOVA, $p = 0.86$) (Figure 8). However, *M. liliana* behaviour was highly variable, when this variability was accounted for (ΔF) there were significant differences in some of the measured behaviours. On average, there was no change in the number of movement events or the total time spent moving in the control, low or mixed treatments (Figure 9a & b). The low and mixed treatments were more variable than the control with clusters of individuals showing no change in movement and 100% increase or decrease. Single sample t-tests showed that there was a significant decrease in number and total time of organism movements after the treatment additions in the high treatments (Figure 9a & b,

respectively). Siphon movement decreased and variability increased from the control to the high treatment (Figure 9c). The change in all treatments except the high was significant. There was an increase in clapping, although not significant, in the control, low and mixed and a decrease in the high treatment (Figure 9d). The response of individuals exposed to the high treatment was less variable than the other treatments (COV = 149) and an outlier in the high treatment skewed the data, affecting results of the single sample t-test.

An important factor determining the effect of *M. liliana* behaviour on the porewater chemistry and flux is the time and degree of sediment pressurisations. Pressurisation of the sediment is caused by feeding, where individuals pump water and material down into their mantle cavity. Pumping rates for the 16 h pre- and 16 h post-treatment addition did not appear to be different across the four treatments (one-way ANOVA, $p > 0.10$) (Figure 10). The variability of pumping rates within each treatment changed after the treatment additions; decreasing in the control (COV from 132 to 116) and high (COV from 123 to 104), compared to increasing variability in the low (COV from 66 to 75) and mixed (COV from 741 to 85). A closer look at feeding behaviours showed that in the 16 h analysed pre- and post-treatment addition there was a decrease in time spent pumping in the control with an overall trend of decreasing total pumping from the L > H > Mx (Figure 11). The response of *M. liliana* pumping to TS was highly variable in the control and the high treatments (COV = 1044 and 2161, respectively) but was much smaller in the low and mixed (COV = 222 & 339, respectively).

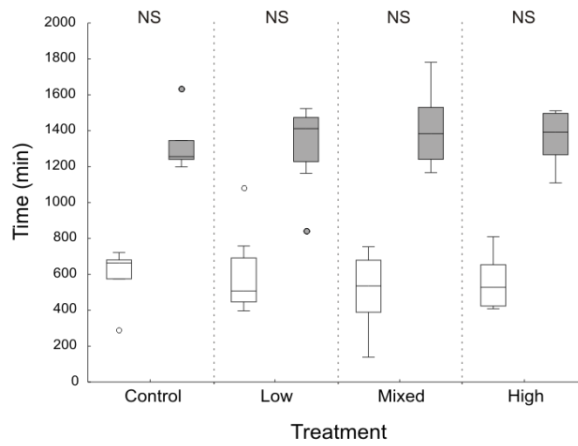


Figure 8: Time inactive (white boxes) and active (grey boxes) in the 16 h post-treatment period analysed. The solid horizontal line is the median, the box represents the 25th and 75th percentiles, the whiskers are the non-outlier range and the circles represent outliers. One-way ANOVA non-significant results are reported as NS.

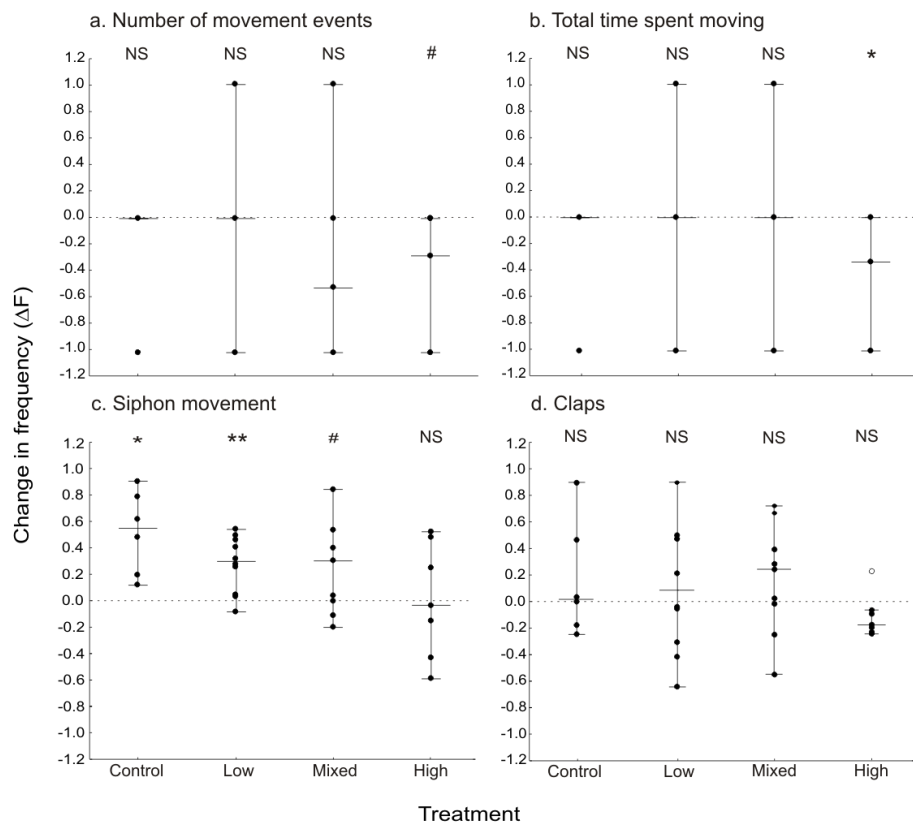


Figure 9: ΔF values for behaviours seen in pressure records. The black dots are the raw data, the solid horizontal line is the median, the whiskers are the non-outlier range and the circles represent outliers. The dashed line highlights no behaviour change pre-/post-treatment; a positive or negative value respectively shows an increase or decrease in behaviour after the treatment additions. Single sample t-test results are reported as; a non-significant result (NS), or a significant result $0.1 < p > 0.05$ (#), $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

Table 5: Treatment averages (± 1 SE) from pressure records for movement events (M #); total time spent moving (M), claps (C) and siphon movement(SM). See Figure 9 for ΔF values.

Behaviour	Treatment Mean \pm SE							
	Control		Low		Mixed		High	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
M #	1.0 ± 0.8	0.0	1.0 ± 0.4	0.3 ± 0.2	2.0 ± 0.7	0.0 ± 0.2	3.0 ± 2.3	0.0 ± 0.1
M (min)	5.0 ± 5.0	0.0	23.6 ± 14.6	6.2 ± 3.2	26.8 ± 8.7	4.5 ± 3.0	70.6 ± 58.3	3.8 ± 3.8
C	66 ± 25	66 ± 15	24 ± 5	97 ± 20	96 ± 23	75 ± 11	121 ± 38	118 ± 22
SM	22 ± 9	61 ± 10	24 ± 5	46 ± 12	29 ± 6	59 ± 14	41 ± 14	40 ± 11

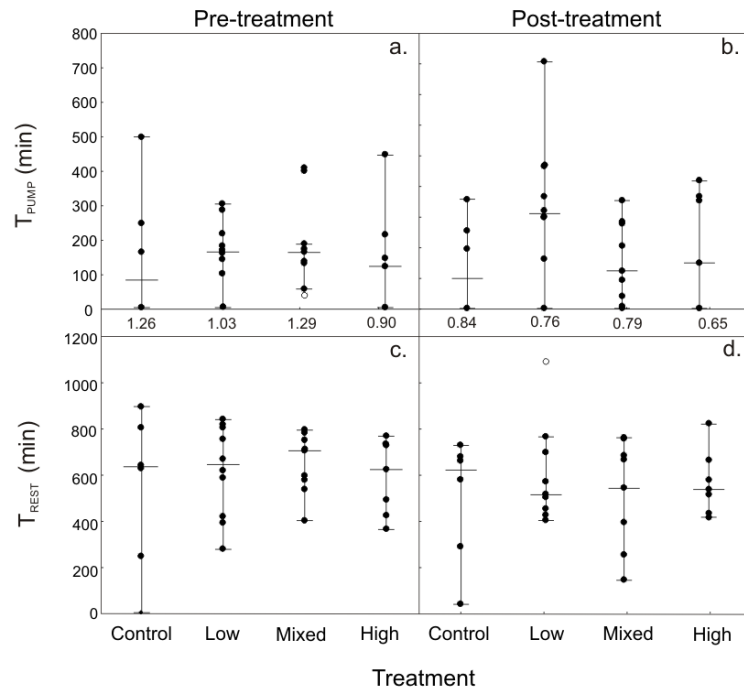


Figure 10: Total time pumping (deposit-feeding and suspension-feeding /ventilating) (a) 16 h pre- and (b) 16 h post-treatment additions, and total time spent resting (c) 16 h pre- and (d) 16 h post-treatment addition. The black dots are the raw data, the solid horizontal line is the median, the whiskers are the non-outlier range and the circles represent outliers, the numbers in the middle are the number of events h^{-1} .

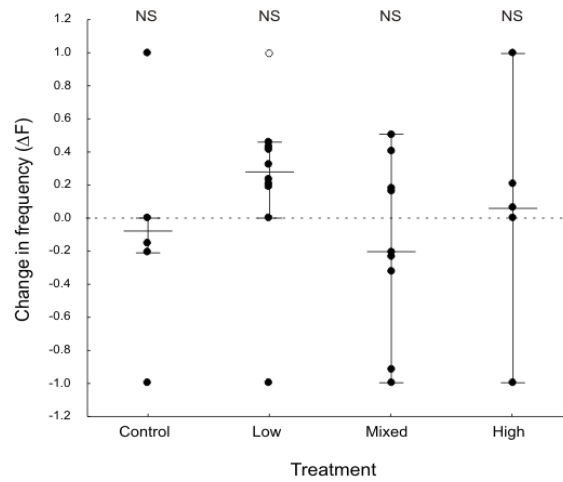


Figure 11: ΔF for time spent pumping from the pressure records. The black dots are the raw data, the solid horizontal line is the median, the whiskers are the non-outlier range and the circles represent outliers. The dashed line highlights no behaviour change pre-/post-treatment, a positive or negative value shows an increase or decrease in total time spent pumping after the treatment additions. Single sample t-test non-significant results are reported as NS.

Feeding behaviour was broken down into deposit-feeding and suspension-feeding/ventilating as the two behaviours affect the porewater fluxes and nutrient recycling in different ways. The low treatment had the greatest change in feeding in response to TS followed by the mixed treatment with a decrease in deposit-feeding and an increase in suspension-feeding/ventilation (Figure 12). Feeding remained unchanged in the control and high treatments, with a median ΔF of 0. The strength of the response in feeding activity decreased from low to high and the variability increased. Both the low and mixed treatments showed a significant reduction in deposit-feeding (Figure 12a & b). In contrast, suspension-feeding/ventilating increased in the low and mixed treatments (Figure 12c & d). The low treatment showed a 20-70% increase in the number and total time of suspension-feeding/ventilating events although significance was only found for the total time. Individuals in the low showed the least amount of variability compared to all other treatments ($L < H < M < C$, $COV = 167, 285, 1046$ and 3526 , respectively).

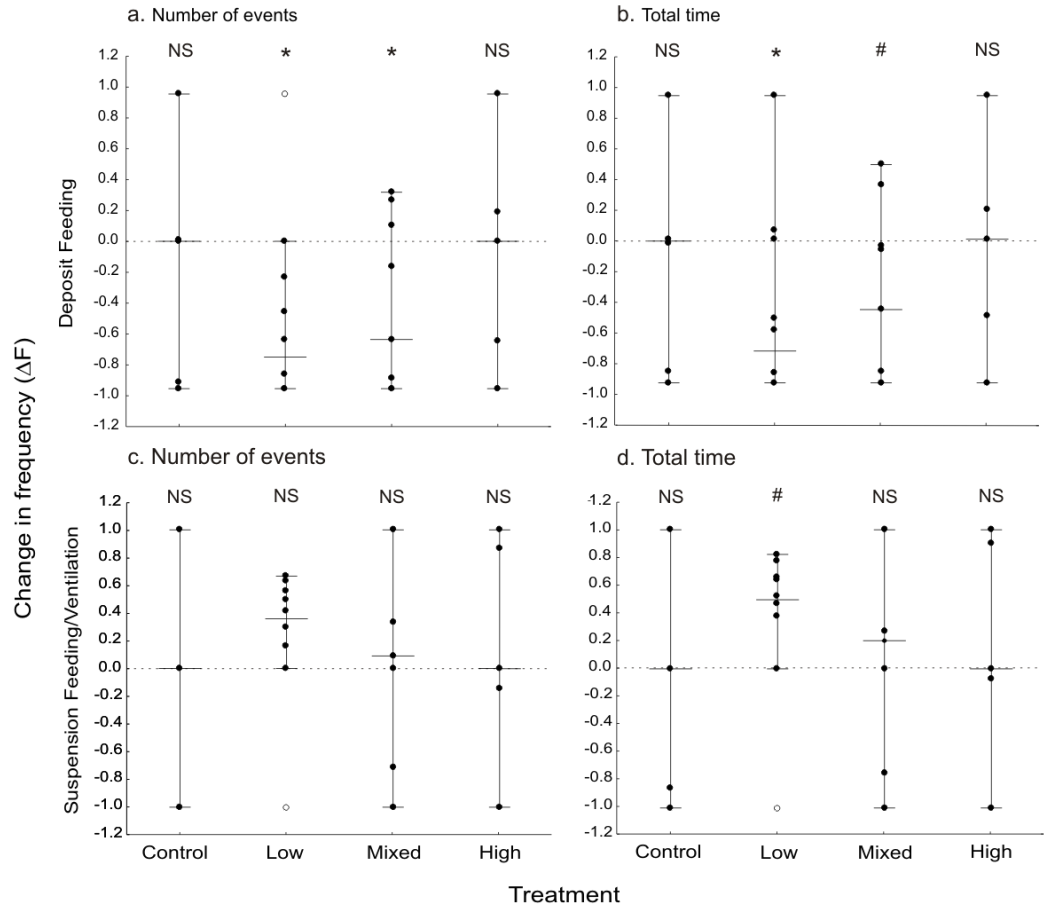


Figure 12: ΔF for deposit-feeding and suspension-feeding/ventilation. The black dots are the raw data, the solid horizontal line is the median, the whiskers are the non-outlier range and the circles represent outliers. The dashed line highlights no behaviour change pre-/post-treatment; a positive or negative value shows respectively an increase or decrease in the number of events or time allocated to feeding behaviour. Single sample t-test results are reported as; a non-significant result (NS), or a significant result $0.1 < p > 0.05$ (#), $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

Table 6: Treatment averages (\pm 1SE) from pressure records for number of deposit-feeding events (DF #), total time spent deposit-feeding (DF), number of suspension-feeding/ventilating events (S/V #) and total time spent suspension-feeding/ventilating (S/V). See Figure 12 for ΔF values.

Behaviour	Treatment Mean \pm SE							
	Control		Low		Mixed		High	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
DF #	19.8 \pm 9.7	11.3 \pm 8.9	12.8 \pm 3.8	3.7 \pm 1.8	17.8 \pm 4.2	9.4 \pm 4.8	12.4 \pm 5.3	6.3 \pm 4.0
DF (min)	119 \pm 59	72 \pm 51	87 \pm 23	36 \pm 19	135 \pm 38	67 \pm 33	96 \pm 43	59 \pm 38
S/V #	0.3 \pm 0.2	2.2 \pm 1.3	3.6 \pm 0.8	8.4 \pm 2.1	2.9 \pm 1.0	3.2 \pm 1.4	2.0 \pm 1.3	4.1 \pm 1.9
S/V (min)	33 \pm 28	50 \pm 31	68 \pm 16	254 \pm 71	53 \pm 18	73 \pm 29	36 \pm 24	109 \pm 51

Video footage indicated that deposit-feeding events were much shorter than suspension-feeding/ventilating events (average of 7 min and 24 min, respectively). To determine if the degree of pressurisation of these two behaviours also varied, the average pressurisation heights between treatments were compared in a two-way ANOVA. The results showed a highly significant interaction between the type of feeding and the treatment ($p = 0.00$). To determine significance a one-way ANOVA and Newman-Keuls post-hoc test comparing deposit-feeding and suspension/ventilation for each treatment was conducted. This showed that there was a significant difference in the degree of pressurisations between deposit-feeding and suspension-feeding/ventilating in the mixed and the high treatments (Figure 13). This was then repeated for deposit feeding across all treatments and suspension-feeding/ventilating across all treatments (Table 7). This analysis showed significantly higher pressurisation in the mixed treatment than all other treatments for both feeding types.

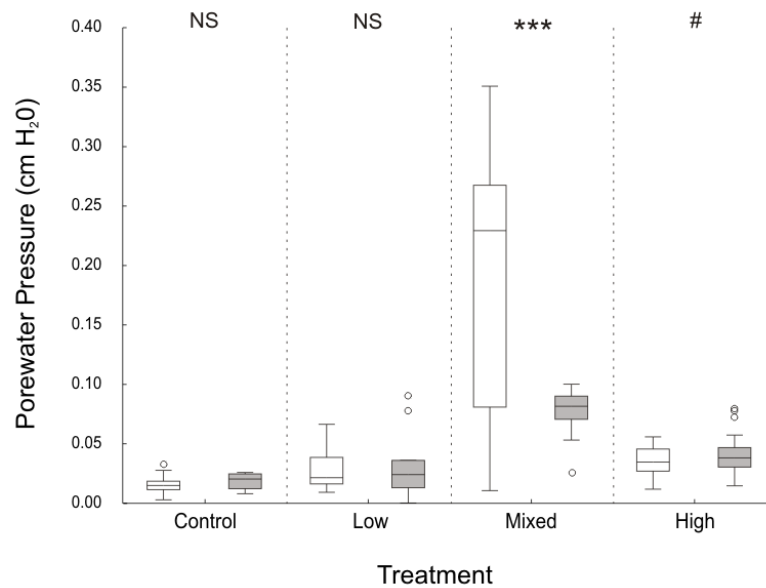


Figure 13: Porewater pressure of feeding bouts measured across the four treatments, post-treatment. The white box is deposit-feeding; the grey box is suspension-feeding/ventilation. The solid horizontal line is the median, the box represents the 25th and 75th percentiles, the whiskers are the non-outlier range and the circles represent outliers. One-way ANOVA comparing deposit-feeding and suspension-feeding/ventilation for each treatment are reported as; a non-significant result (NS), or a significant result $0.1 < p < 0.05$ (#), $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

Table 7: Comparison of average pressurisation heights (\pm 1SE) (cm H₂O) of deposit-feeding (DF) and suspension-feeding/ventilation (S/V) between experimental treatments showing mean \pm standard error, one way ANOVA p value and results of Newman-Keuls post-hoc tests (C= control, L= low, Mx= mixed and H =high).

Variable	Treatment Mean \pm SE				ANOVA p	Post hoc
	Control	Low	Mixed	High		
DF	0.016 \pm 0.001	0.036 \pm 0.006	0.185 \pm 0.011	0.036 \pm 0.002	0.0000	C = L = H < Mx
S/V	0.018 \pm 0.002	0.036 \pm 0.006	0.086 \pm 0.010	0.041 \pm 0.003	0.0001	C = L = H < Mx

CHAPTER FOUR: DISCUSSION

This was the first time that a controlled laboratory experiment, with a comparatively high level of replication, has been used to explore the effects of thin deposits of aged terrigenous sediment (TS) on a key benthic species. The goal was to address the impact of aged TS on the behaviour of *M. liliana* and link changes in behaviour to potential changes in porewater flux and ecosystem functioning. Three TS treatments were chosen to simulate the on-going addition of small amounts of TS and its incorporation into the marine environment. The low treatment (1 mm surface layer) represented the initial deposition of TS, the high treatment (4 mm surface layer) represented its build up over time and the mixed treatment (the equivalent of the high treatment mixed through the top 2 cm) represented its incorporation into marine sediments. Behaviour was assessed by surface activity via time-lapse cameras, and sub-surface by high resolution pressure sensors pre- and post-treatment addition. The addition of TS significantly modified the sediment surface properties. Subtle but significant effects of the treatments on some behaviour were determined; although they were not necessarily consistent between observation methods or level of treatment.

4.1 Sediment parameters

The physical characteristics of TS differed from marine sediment and so the addition of TS significantly modified the sedimentary environment of the mesocosms. TS caused a reduction in hydraulic conductivity, with an order of magnitude decrease for the TS addition mixed through the sediment compared to its unmixed equivalent. TS eroded off the land and deposited in estuaries is often small in size with a high proportion of silt/clay sized particles that are enriched in organic material (Norkko et al. 2002). As a result there was a significant increase in silt/clay and organic content with increasing TS. Microphytobenthos (measured as sediment chlorophyll *a* concentration) is a source of food for *M. liliana* and although the mixed treatment had significantly lower concentrations, all measurements were within ranges *M. liliana* commonly experience in the field (Woodin et al. 2012).

4.2 Behavioural analysis

The deposition of thin layers of TS significantly modified the sedimentary environment and this caused subtle changes in *M. liliana* behaviour. Video footage showed the greatest behavioural response in the high treatment, whereas data from the pressure sensors showed individuals exposed to the low and mixed treatments had a stronger response. There was a reduction in activity that bioturbated the sediment surface with significant decreases in siphon relocation, clapping and deposit-feeding. Feeding behaviours were significantly altered in the low and mixed treatments, with reduced deposit-feeding and increased suspension-feeding/ventilation, suggesting a switch in feeding modes. Additionally, the degree of pressurisation during feeding significantly increased in the mixed and high treatments.

The time-lapse imagery of surface and hydrostatic pressure reading of sub-surface behaviour were complimentary and shed light on slightly different aspects of *M. liliana* behaviour. The pressure records picked up activity not observable from the sediment surface, while the video footage showed the effect of behaviours on the sediment surface, and by no means were they expected agree 100% of the time. The differences in behaviours observed in the two methods highlights that a complementarity of approaches is important for understanding cryptic infaunal species which are hard to study.

4.2.1 Surface activity

Importantly, no significant changes in surface activity were measured in the control. I can, therefore confidently conclude that all changes in behaviours can be attributed to the experimental treatment effects and were not a function of time spent in the mesocosms. The addition of TS caused a significant increase in the number of siphon movements across all treatments. Siphon movement was classified as the inhalant/exhalant siphon moving in and out the sediment. The siphon did not make contact with the sediment surface, so was not deposit-feeding, and movements were rapid with minimal time spent in the water column, so were not suspension-feeding/ventilation. An increase in siphon movement therefore had

no observable effect on the sediment surface but may have had long-term physiological effects on *M. liliana* with respect to energy expenditure. Apart from siphon movement, all other behaviours observed at the surface effectively bioturbated the sediment. Bioturbation by macrofauna is known to influence sediment stability (e.g. Rhoads 1982; Grant and Daborn 1994; de Deckere et al. 2001; Lelieveld et al. 2004) and increase erodability, by reducing sediment compaction, increasing water content of sediment (Gerdol and Hughes 1994), producing and depositing faecal pellets (Andersen 2001; Andersen et al. 2002).

Siphon relocation is essentially the animal foraging for suitable feeding locations; if an area is not suitable it will relocate and try again (Woodin et al. 2012). The relocation of the inhalant siphon was observed as a new hole opening up in the sediment surface and the relocation of the exhalant siphon was observed as a change in the location of the accumulation of faecal pellets. This activity bioturbated the sediment surface pre-treatment addition however, siphon relocation was reduced significantly with the addition of TS. Reduced siphon relocation would therefore decrease the re-working of sediments, reducing sediment erodability and the capacity for TS to be transported away and incorporated into marine sediments, especially in an area with low physical disturbance. As a result, TS would be more persistent and may have long term effects on *M. liliana*. Changes in siphon relocation have been noted previously, although observations were of increased siphon relocation with increasing silt/clay (Woodin et al. 2012). These observations were made over a shorter time scale (5 h) and may have only captured the initial response of *M. liliana* to the disturbance.

Two different feeding behaviours were identified in the video footage of the sediment surface; deposit-feeding and suspension-feeding/ventilation. Deposit-feeding bioturbated the sediment surface, leaving feeding tracks, whereas suspension-feeding/ventilation made no contact with the sediment surface. There was no significant change in deposit-feeding observed from the sediment surface and therefore bioturbation by deposit-feeding remained constant. This would have assisted the removal and mixing of TS into ambient sediment. In contrast, suspension-feeding/ventilation increased significantly with increasing TS. This may have been a response to lower sediment oxygen concentrations or to avoid

unfavourable conditions at the sediment surface. Suspension-feeding/ventilation did not bioturbate the surface sediment and therefore there were no observable effects at the surface, however it was important in terms of sediment pressurisations (discussed in section 4.2.2). The clean, aquaria grade, salt water used in all of the experiments did not contain nutritious particles and therefore there would have been no uptake of particulate matter during suspension-feeding/ventilation. Deposit-feeding was unchanged by the addition of TS, it was therefore assumed that there would have been no change in the uptake of particulate matter, and a constant rate of sediment processing was maintained.

Clapping was comprised of coughing, pseudofaeces production and defecation, all of which are associated with the removal of unwanted material during sediment processing on the gill or digestion. TS has a high inorganic fraction that has no nutritional value and has been shown to increase pseudofaeces production (Taghon and Jumars 1984; Jumars and Wheatcroft 1989; Ellis et al. 2002; Safi et al. 2007). Therefore, if a constant feeding rate was maintained I had expected an increase in clapping with the addition of TS which does not get digested. Contrary to expectations, clapping was significantly reduced in the high treatment and although not significant some individuals in the low and mixed TS treatments showed reduced clapping, despite a constant rate of sediment processing being maintained pre- and post-treatment addition. Reducing clapping may have been a mechanism to save energy and in the long run may have caused detrimental effects to individual condition. As with reduced siphon relocation, reduced clapping would reduce the re-working of TS into marine sediments and its transportation away from the affected area, thereby possibly prolonging its existence in the environment and the stress it places on *M. liliana*.

4.2.2 Hydraulic activity

M. liliانا showed a range of hydraulic activities that caused behaviour specific pressure signals. Pressure signals associated with siphon movement and clapping had a large amplitude but were short in duration and the time integrated pressures of these behaviours have been shown to be of little importance for driving porewater flux (Volkenborn et al. under review). The number of siphon movements recorded sub-surface increased significantly with the addition of TS and this agreed with observations of surface behaviour. Additionally, the effect of time on this result could not be ruled out, as there was also a significant increase in siphon movement measured in the control. In contrast, although much smaller in magnitude, sediment pressurisation during feeding is longer in duration than siphon movement and clapping and the time integrated effect on sediment pressure is important in driving porewater advection (Volkenborn et al. under review).

The pumping activity of bivalves during feeding is important in driving porewater fluxes and sediment oxygen dynamics (Woodin et al. 2010). Contrary to my predictions there was no significant change in total pumping (feeding) with the addition of TS. The TS additions used in this experiment were very small and within the ranges that *M. liliانا* naturally inhabit. Results indicate that the subtle differences in surface sediment caused by the additions of small amounts of TS are not likely to elicit a change in the pumping rates of *M. liliانا* over a 24 h period. Consequently, we would not expect to see a change in porewater flux associated with the pressurisation during feeding. If the observation period was extended I may have seen long-term effects on *M. liliانا* feeding. The two feeding behaviours observed in the surface images (deposit-feeding and suspension-feeding/ventilation) both pressurised the sediment at depth, but differed in the temporal patterns of pressurisations (7 min and 25 min on average, respectively).

There were significant changes in the number of events and time allocated to each feeding mode (deposit-feeding and suspension-feeding/ventilation) post-treatment. A switch in feeding mode from deposit-feeding to suspension-feeding/ventilation was observed in the pressure records from the low and mixed treatments (Figure 13). An increase in periods of pressurisations without obvious

uptake of sediment particles were also observed in *M. liliana* by Volkenborn et al (under review). Switches of feeding modes in response to changes in environmental conditions are common in Tellinid bivalves. *Macoma balthica* are known to deposit-feed in muddy, fine sediments but suspension-feed in sandy sediments (Olafsson 1986). In addition, the time spent suspension-feeding has also been found to increase at high densities (Marinelli and Williams 2003) and when the availability of food in the water column is high (Hummel 1985; Lin and Hines 1994). Deposit-feeding dominates in *Macoma nasuta*, *Macoma secta* and *Macoma inquinata* in low flow velocities but as flow speed increases there is a switch to suspension-feeding (Levinton 1991).

In this study, it was impossible to distinguish between suspension-feeding and ventilating, but based on two facts I suggest that *M. liliana* are ventilating rather than suspension-feeding. Firstly, clean aquaria grade salt water was used in all experiments, therefore there were no suspended particulates for *M. liliana* to feed on. Secondly, during experimental breakdown it was noted that just below the sediment surface was very anoxic (pers.obs.). TS layers are known to affect the availability of oxygen by decreasing permeability and thus impeding advective solute transport (Huettel and Webster 2001). Increasing ventilation may have been a behavioural mechanism to cope with low oxygen. Increasing suspension-feeding/ventilation and decreasing deposit-feeding will have important implications for sediment stability. *M. liliana* bioturbate the sediment surface during deposit-feeding and destabilise the sediment making it easier to erode. A reduction in deposit-feeding and increase in suspension-feeding/ventilation (not bioturbating) may help retain the thin layers of TS and this may have long term consequences for *M. liliana* condition.

A switch in feeding modes may also affect the geochemical conditions within the sediment. Feeding patterns in this study were similar to those previously observed, where feeding events occurred in blocks followed by periods of resting, during which the hydrostatic pressure returned to baseline (Volkenborn et al. under review). Sediment oxygen dynamics have been directly related to pressurisations produced by the feeding patterns of *M. liliana*; pockets of sediment surrounding the exhalant siphon was oxygenated during feeding bouts and was consumed during resting periods, resulting in oscillations from oxic to

anoxic conditions (Volkenborn et al. under review). A switch to more suspension-feeding/ventilating, which occurs on a much longer time scale compared to deposit-feeding (in a 16 h period 4 h more oxygenation), would mean that there would be greater oxygenation of sediments. This may counteract the anoxia caused by the TS layers and all oxygen may not be completely consumed during non-pressurised periods, resulting in more stable geochemical conditions. Sediments with oscillatory geochemical conditions on the scale of hours to day's drive higher mineralization rates of organic matter than those with stable redox conditions (Sun et al. 1993; Aller 1994; Sun et al. 2002; Caradec et al. 2004; Cravo-Laureau et al. 2011; Bennett et al. 2012). Oscillations on shorter scales (minutes) generated by *M. liliana* feeding are likely to have the same effect (Volkenborn et al. under review). An increase in suspension-feeding/ventilation could therefore potentially reduce the recycling of organic material by creating more stable geochemical conditions potentially affecting primary productivity.

A switch from deposit-feeding to suspension-feeding/ventilation will also affect the functionality of benthic communities. Although deposit-feeding and suspension-feeding/ventilation both cause a pressurisation of the sediment, which creates oxic pockets and drives bioadvective flows, the two feeding modes have different functionalities in terms of how they affect the sediment surface. Deposit feeders disturb the sediment surface, increasing the surface area for solute exchange (Huettel and Gust 1992), destabilises the sediment bed and re-suspends fine particulate matter (Lelieveld et al. 2004), which has implications for faunal recruitment (Marcus and Schmidt-Gengenbach 1986). This activity oxygenates surface sediments, increases the release of nutrients from the sediments for primary productivity and assists the transportation of fine particulate matter (Lelieveld et al. 2004). In contrast, suspension feeders filter fine particulates out of the water column and deposit them on the sediment surface, thereby increasing water quality and delivering organic material to the benthos where it is recycled into inorganic nutrients (Ostroumov 2005). Hence a change in feeding modes will have important implications for water clarity and nutrient recycling, which may lead to a change in the functionality of the community.

The amplitude of sediment pressurisation during feeding was affected by the addition of TS and the distance away from the pressure sensor. The further away

from a sensor *M. liliana* were the weaker the signal measured (Wethey et al. 2008). If movement had changed significantly during the course of the experiment, comparison of signal amplitudes may have been misleading. There were no significant differences in *M. liliana* movement in the control or any of the treatments, and therefore it was assumed that *M. liliana* remained within the vicinity of original placement. This allowed the comparison of post-treatment pressurisations without distance aliasing results. Pressurisation of the sediment during deposit-feeding and suspension-feeding/ventilation was significantly higher (5 and 2× greater, respectively) in the mixed treatment compared to all other treatments. This is likely related to the decrease in hydraulic conductivity due to TS capping and pore clogging by silt/clay, resulting in the build-up of pressure. Higher pressurisations would drive a greater flux of porewater with the potential to oxygenate a larger volume of sediment. However, if permeability is reduced then a higher pressurisation is needed to drive the same volume of flow. Therefore although the mixed treatment increases the potential porewater flux this may be counteracted by the decrease in permeability and increased pressure may not have translated into increased flux. As well as affecting the porewater fluxes, reduced hydraulic conductivity could also affect its spatial patterns. The response of porewater to sediment pressurisation by *M. liliana* is governed by sediment permeability and hydraulic conductivity. Porewater flows through paths of least resistance, therefore when the sediment is capped it may flow out through cracks in the sediment surface resulting in jet-like movements, rather than the sheet-like movements that you see in permeable sediments (Woodin et al. 2010). Alternatively, rather than displacing water directly above the animal, porewater may flow radially at depth away from the organism and displace water at the surface further away, where there is less resistance to flow (i.e. no TS layer at the surface).

As well as affecting the mode of feeding, TS also affected the amplitude of the different feeding modes within the mixed and high treatments. Pressurisation during deposit-feeding was significantly higher than pressurisation during suspension-feeding/ventilation (twice the amplitude) in the mixed treatment. Differences in the amount of pressurisations between feeding modes will have important implications for porewater flow. In the mixed treatment there was a

significant decrease in deposit-feeding and an increase in suspension-feeding/ventilation. A decrease in deposit-feeding would result in a smaller porewater flux and a smaller volume of sediment would be affected. Conversely, suspension-feeding/ventilation in the high treatment produced marginally greater pressurisation than deposit-feeding. Feeding in the high treatment remained on the whole unchanged. However, if suspension-feeding/ventilation were to increase, as it did in the other treatments, then higher pressurisations would drive greater porewater flux, and as a result a greater volume of sediment would be affected. Additionally, stronger pressurisations during suspension-feeding/ventilation, which had longer durations, may promote more stable geochemical conditions by increasing sediment oxygenation.

As previously mentioned, I expected that clapping would increase if a constant feeding rate was maintained. Total pumping of *M. liliana* was not significantly changed by the addition of TS but there was a decrease in deposit-feeding and an increase in suspension-feeding/ventilation in the low and mixed treatments. No particulate matter would have been ingested during suspension-feeding/ventilation; therefore there would have been less sediment to process which may be why we did not see a significant change in clapping. In the high treatment, clapping decreased and although not significant the variability was much smaller than responses in the other treatments, which agreed with surface observations. Changes in clapping behaviour were inconsistent across treatments but have important implications for sediment stability and erodability. As described previously, decreased clapping will increase sediment stability, which increases the retention of TS, whereas an increase in clapping will decrease sediment stability and assist the removal and/or incorporation of TS into marine sediments.

The behaviour of *M. liliana* was highly variable in both the video and pressure sensor data. Bivalves are known to show considerable physiological and behavioural plasticity in relation to varying seston quantities and qualities (Olafsson 1986; Iglesias et al. 1992; Miller et al. 1992; Lin and Hines 1994; Wong and Cheung 1999; Norkko et al. 2006). Interestingly for the majority of behaviours the variability in response decreased with increasing TS. On a population level, this may have important consequences for porewater flow and geochemical conditions of large areas. If when exposed to TS individuals within a

population move towards adopting a similar set of behaviours, then on a whole the population may lose function and the effects of TS would occur at a much larger spatial and temporal scale. For example, results here have indicated that there tends to be less bioturbating activity with the addition of TS. If an entire population showed this then sediment erodability might drastically decrease, and TS may be able to build up to levels examined in Lohrer et al. (2004) and Rodil et al. (2011), which reduced biodiversity and ecosystem functioning.

4.3 Limitations

This study is new and novel, as it was the first time that simplified mesocosms have been used in a laboratory setting to assess the effects of TS on the behaviour of *M. liliانا*. From the measured changes in behaviour, I was able to suggest potential implications for porewater flux and ultimately ecosystem functioning. The credibility of findings from scaling up mesocosm experiments to an ecosystem level is often questioned. However, this approach has become more common as it provides a mechanistic understanding of ecological processes, which, through the traditional route of experimental manipulation, would otherwise be hard to gain due to extensive temporal and spatial scales. (Benton et al. 2007; Braeckman et al. 2010).

Food availability is known to modify the behaviour of deposit feeders (Taghon and Jumars 1984) and could have affected behavioural responses to TS in *M. liliانا*. In this experiment, ambient microphytobenthos (measured as sediment chlorophyll *a* concentration) during collection and bacteria attached to sediment particles was the only food source for *M. liliانا*. Although the mixed treatment had significantly lower concentrations of chlorophyll *a* (bacterial biomass was not measured), all concentrations were within ranges commonly experienced by *M. liliانا* in the field (Woodin et al. 2012), therefore the availability of food should not have affected *M. liliانا* behaviour. I collected the sediment for all of the experiments on the same day to avoid differences in the sediment properties, as the experiments were ran over several months. Once collected, the sediment was sieved, frozen and defrosted as needed; these processes may have affected the quality of food, which may have influenced the behaviour of *M. liliانا*. To avoid this, the sediment would have to be collected fresh for each experiment however, sediment properties may then change over the duration of the experiments and this

could influence *M. liliana* behaviour. Additionally, the handling and transportation of bivalves can cause stress which can modify behaviour (Putman 1995). I took measures to minimise the stress on *M. liliana* during collection, transportation and relocation, although this process undoubtedly would have affected *M. liliana* and may have their behaviour. Therefore to remove this bias from our experiment only animals that buried naturally were used in the experiment and the first 12 h of data collected was not analysed to allow *M. liliana* to re-establish “normal” behaviour before data collection. Additionally, post-treatment burial times were similar, showing animals were unlikely to have been stressed in any of the treatments.

This study captured only short-term behaviour changes (24 h of post-treatment data collection) in a simplified environment. Bivalve feeding can change in a matter of hours or days in response to increased TS (Hawkins et al. 1996). Although these temporal patterns were accounted for, the small amount of TS added may have prolonged the response time. If the observation period was increased, I may have seen other changes in behaviour or there may have been long-term physiological consequences associated with stress from the TS. The short period of data collection was chosen to minimise stress on *M. liliana*, so that condition was not significantly affected over the duration of the observation period, therefore potential long-term effect of TS on *M. liliana* behaviour was not within the scope of this experiment. Additionally, the experiment generated large data-sets, which were time consuming to analyse and the project did not allow for longer periods of data collection. The ability to process data also limited the level of replication that was logistically feasible. By conducting the experiment in simplified mesocosms I was able to have higher levels of replication than those in previous studies looking at the same stressor (Woodin et al. 2012). However, measured behaviour was highly variable in both the control and the TS treatments. If replication was increased, the variability may have been reduced and more significant changes in behaviour in response to TS may have been seen.

In the past, studies looking at the effect of infaunal activity on porewater fluxes have measured porewater flows directly, using ultra sounds (Wetthey and Woodin 2005) or indirectly using oxygen optode imagery, relating oxygen dynamics to porewater flow (Polerecky et al. 2006; Volkenborn et al. 2010; Woodin et al.

2010). No measurements of porewater flux were made in this study, due to the experimental set-up, thus I could only speculate how porewater flux would be affected by the observed changes in behaviour.

4.4 Summary of major findings

I measured changes in *M. liliana* behaviour in response to thin deposits of TS by observing surface activity and sub-surface changes in the hydraulic activities of *M. liliana*. The TS additions used in this experiment were sub-lethal, as they were within ambient ranges that *M. liliana* experience and the TS was not completely foreign, it was aged with a marine signature. The TS treatments caused subtle changes in *M. liliana* behaviour that were not always consistent across treatments or methods.

The major findings of the experiment were:

1. TS significantly modified the properties of surface sediment. The most important change, in terms of influencing sediment pressurisation and porewater flux was hydraulic conductivity. This decreased significantly with increasing TS and was an order of magnitude lower when TS was mixed through the top 2 cm of sediment.
2. The addition of small amounts of TS caused subtle changes in surface behaviour of *M. liliana*. Siphon movement increased, whereas siphon relocation and clapping decreased. Deposit-feeding was unchanged but there were significant increases in suspension-feeding/ventilation across all TS treatments.
3. Changes in surface activity reduced the bioturbation of surface sediments, which decreased the surface erodability and this helped to retain the TS layers. As a result, TS may cause long-term degradation of individual condition, population fitness and ultimately ecosystem functioning.
4. The addition of TS caused a switch in feeding modes from deposit-feeding to suspension-feeding/ventilation. This changed the temporal patterns of sediment pressurisation (the duration of suspension-feeding/ventilation events was on average 3 times longer than deposit-feeding events), which is linked to sediment oxygen dynamics. More suspension-feeding/ventilation

will cause longer periods of pressurisation, which will increase sediment oxygenation and stabilise geochemical conditions. This is likely to reduce nutrient recycling and estuarine productivity. As with surface observations, reduced deposit-feeding will also have important implications for sediment stability and the retention of TS.

5. The amplitude of sediment pressurisation during feeding was significantly higher in the mixed treatment compared to the other treatments, which is likely to be an effect of reduced hydraulic conductivity. Greater pressurisation of the sediment would cause larger porewater fluxes which could potentially affect a larger volume of sediment.
6. The height of pressurisation during deposit-feeding was twice that measured during suspension-feeding/ventilation in the mixed treatment. As a result, I would expect the magnitude of porewater flux during deposit-feeding to be twice as large as a porewater flux during suspension-feeding/ventilation. This paired with the different temporal scales of the two feeding modes and the observed switches in feeding modes would have important consequences for porewater fluxes and geochemical conditions. Rather than short periods of high pressurisation there would be longer periods of smaller pressurisations. This is likely to drive smaller porewater fluxes and may promote stable geochemical conditions, thereby reducing productivity.

4.5 Future work

Through their hydraulic behaviours, *M. liliانا* affect sediment pressurisation, and therefore behavioural changes elicited by TS could play an important role in porewater flux and ecosystem function. The functioning of estuaries is a complex process. However, the basis of functionality at some fundamental level goes back to individual behaviour, thus developing the link between behaviour and ecological processes is vital if we are to understand how estuarine functioning is affected by TS. This is a useful preliminary study that shows TS can cause subtle changes in the hydraulic activity of *M. liliانا*, which could potentially affect porewater fluxes.

To improve the scope of this study and strengthen the link between *M. liliana* behaviour and ecosystem functioning, I suggest future work include field experiments, which in addition to using time-lapsed imagery and pressure sensors, should measure porewater movement. To capture the high variability in behaviour I suggest higher levels of replication and an increased observation period, as I only looked at short-term behaviour. The long-term effects of TS need to be determined; this could be achieved by collecting data after different exposure times (i.e.; every day for a week and then again a month later) and analysing condition after several months of exposure to TS. This experiment highlighted the influence of grain size on bioadvective flows, thus future work should look at incorporating a sediment gradient from a sandy site to a muddy site. Site exposure to wave energy is an important factor in determining the retention of TS, which will likely influence the effect on *M. liliana* behaviour and condition. Therefore, it will also be useful to look at sites of different exposures. Increasing replication and the duration of experiments will produce large data-sets, and to reduce the time required to analyse these I suggest focusing on only feeding and movement. These behaviours have shown the potential to drastically modify porewater flux and bioturbate sediments both of which are important for benthic-pelagic coupling. This will allow the identification of changes in *M. liliana* behaviour and condition in response to TS, as well as its affects at the population level, to determine the long-term effects on ecosystem functioning.

REFERENCES

- Aller RC (1994) Bioturbation and reimeralization of sedimentary organic-matter-effects of redox oscillation. *Chemical Geology* 114: 331-345
- Andersen TJ (2001) Seasonal variation in erodibility of two temperate, microtidal mudflats. *Estuarine Coastal and Shelf Science* 53: 1-12
- Andersen TJ, Jensen KT, Lund-Hansen L, Mouritsen KN, Pejrup M (2002) Enhanced erodibility of fine-grained marine sediments by *Hydrobia ulvae*. *Journal of Sea Research* 48: 51-58
- Ball DF (1964) Loss-on-ignition as an estimate of organic matter and organic carbon in non-calcareous soils. *Journal of Soil Science* 15: 84-92
- Beaumont NJ, Austen MC, Atkins JP, Burdon D, Degraer S, Dentinho TP, Derous S, Holm P, Horton T, van Ierland E, Marboe AH, Starkey DJ, Townsend M, Zarzycki T (2007) Identification, definition and quantification of goods and services provided by marine biodiversity: Implications for the ecosystem approach. *Marine Pollution Bulletin* 54: 253-265
- Bell RG, Hume TM, Dolphin TJ, Green MO, Walters RA (1997) Characterisation of physical environmental factors on an intertidal sandflat, Manukau Harbour, New Zealand. *Journal of Experimental Marine Biology and Ecology* 216: 11-31
- Bennett WW, Teasdale PR, Panther JG, Welsh DT, Zhao H, Jolley DF (2012) Investigating arsenic speciation and mobilization in sediments with DGT and DET: A mesocosm evaluation of oxic-anoxic transitions. *Environmental Science & Technology* 46: 3981-3989
- Benton TG, Solan M, Travis JMJ, Sait SM (2007) Microcosm experiments can inform global ecological problems. *Trends in Ecology & Evolution* 22: 516-521
- Blackburn TH (1988) Methods for measuring rates of NH_4^+ turnover in anoxic marine sediments, using a ^{15}N - NH_4^+ dilution technique. In: Blackburn TH, Sorensen J (eds) *Nitrogen cycling in coastal marine environments*. John Wiley and Sons for SCOPE and ICSU, Chichester, pp 175-190
- Bonsdorff E, Blomqvist EM, Mattila J, Norkko A (1997) Coastal eutrophication: Causes, consequences and perspectives in the Archipelago areas of the northern Baltic Sea. *Estuarine, Coastal and Shelf Science* 44, Supplement 1: 63-72
- Boudreau BP (1998) Mean mixed depth of sediments: The wherefore and the why. *Limnology and Oceanography* 43: 524-526
- Braeckman U, Provoost P, Gribsholt B, Van Gansbeke D, Middelburg JJ, Soetaert K, Vincx M, Vanaverbeke J (2010) Role of macrofauna functional traits

- and density in biogeochemical fluxes and bioturbation. *Marine Ecology-Progress Series* 399: 173-186
- Campbell SJ, McKenzie LJ (2004) Flood related loss and recovery of intertidal seagrass meadows in southern Queensland, Australia. *Estuarine, Coastal and Shelf Science* 60: 477-490
- Caradec S, Grossi V, Gilbert F, Guigue C, Goutx M (2004) Influence of various redox conditions on the degradation of microalgal triacylglycerols and fatty acids in marine sediments. *Organic Geochemistry* 35: 277-287
- Cassie RM, Michael AD (1968) Fauna and sediments of an intertidal mud flat: A multivariate analysis. *Journal of Experimental Marine Biology and Ecology* 2: 1-23
- Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. *Science* 279: 555-558
- Cravo-Laureau C, Hernandez-Raquet G, Vitte I, Jézéquel R, Bellet V, Godon J-J, Caumette P, Balaguer P, Duran R (2011) Role of environmental fluctuations and microbial diversity in degradation of hydrocarbons in contaminated sludge. *Research in Microbiology* 162: 888-895
- Cummings V, Thrush S, Hewitt J, Norkko A, Pickmere S (2003) Terrestrial deposits on intertidal sandflats: sediment characteristics as indicators of habitat suitability for recolonising macrofauna. *Marine Ecology-Progress Series* 253: 39-54
- Cummings V, Vopel K, Thrush S (2009) Terrigenous deposits in coastal marine habitats: influences on sediment geochemistry and behaviour of post-settlement bivalves. *Marine Ecology-Progress Series* 383: 173-185
- Cummings VJ, Thrush SF (2004) Behavioural response of juvenile bivalves to terrestrial sediment deposits: implications for post-disturbance recolonisation. *Marine Ecology-Progress Series* 278: 179-191
- Davison D, Hughes D (1998) *Zostera* biotopes. Volume I. An overview of dynamics and sensitivity characteristics for conservation management of marine SACs. Marine SACs Project, UK, Scottish Association for Marine Science
- Day P (1965) Methods of soil analysis. In: Black C (ed) Particle fractionation and particle-size analysis. American Society of Agronomy, Madison, Wiscousin, pp 545-567
- de Deckere EMGT, Tolhurst TJ, de Brouwer JFC (2001) Destabilization of cohesive intertidal sediments by infauna. *Estuarine, Coastal and Shelf Science* 53: 665-669
- Dolphin TJ, Hume TM, Parnell KE (1995) Oceanographic processes and sediment mixing on a sand flat in an enclosed sea, Manukau Harbour, New Zealand. *Marine Geology* 128: 169-181

- Ellis J, Cummings V, Hewitt J, Thrush S, Norkko A (2002) Determining effects of suspended sediment on condition of a suspension feeding bivalve (*Atrina zelandica*): results of a survey, a laboratory experiment and a field transplant experiment. *Journal of Experimental Marine Biology and Ecology* 267: 147-174
- Forster S, Huettel M, Ziebis W (1996) Impact of boundary layer flow velocity on oxygen utilisation in coastal sediments. *Marine Ecology-Progress Series* 143: 173-185
- Gargas E (1972) Measurements of microalgal primary production (phytoplankton and microbenthos) in the Smålandshavet (Denmark). *Ophelia* 10: 75-89
- Gerdol V, Hughes RG (1994) Effect of *Corophium volutator* on the abundance of benthic diatoms, bacteria and sediment stability in two estuaries in southeastern England *Marine Ecology Progress Series* 114: 109-115
- Glud RN (2008) Oxygen dynamics of marine sediments. *Marine Biology Research* 4: 243-289
- Glud RN, Forster S, Huettel M (1996) Influence of radial pressure gradients on solute exchange in stirred benthic chambers. *Marine Ecology-Progress Series* 141: 303-311
- Grant J, Daborn G (1994) The effects of bioturbation on sediment transport on an intertidal mudflat. *Netherlands Journal of Sea Research* 32: 63-72
- Gray JS (1997) Marine biodiversity: Patterns, threats and conservation needs. *Biodiversity and Conservation* 6: 153-175
- Haese RR, Pronk GJ (2011) Intra-annual variability in primary producer groups and nitrogen dynamics in an intermittently closed estuary exposed to mediterranean climate. *Estuaries and Coasts* 34: 557-568
- Hawkins AJS, Smith RFM, Bayne BL, Heral M (1996) Novel observations underlying the fast growth of suspension-feeding shellfish in turbid environments: *Mytilus edulis*. *Marine Ecology Progress Series* 131: 179-190
- Herman PMJ, Middelburg JJ, Van de Koppel J, Heip CHR (1999) Ecology of estuarine macrobenthos. In: Nedwell DB, Raffaelli DG (eds) *Advances in Ecological Research*, Vol 29: Estuaries. Elsevier Academic Press Inc, San Diego, pp 195-240
- Hewawasam T, von Blanckenburg F, Schaller M, Kubik P (2003) Increase of human over natural erosion rates in tropical highlands constrained by cosmogenic nuclides. *Geology* 31: 597-600
- Hewitt JE, Cummings VJ, Ellis JI, Funnell G, Norkko A, Talley TS, Thrush SF (2003) The role of waves in the colonisation of terrestrial sediments deposited in the marine environment. *Journal of Experimental Marine Biology and Ecology* 290: 19-47

- Hewitt JE, Pilditch CA (2004) Environmental history and physiological state influence feeding responses of *Atrina zelandica* to suspended sediment concentrations. *Journal of Experimental Marine Biology and Ecology* 306: 95-112
- Hewitt JE, Thrush SF, Cummings VJ, Pridmore RD (1996) Matching patterns with processes: Predicting the effect of size and mobility on the spatial distributions of the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. *Marine Ecology-Progress Series* 135: 57-67
- Huettel M, Gust G (1992) Impact of bioturbation on interfacial solute exchange in permeable sediments *Marine Ecology Progress Series* 89: 253-267
- Huettel M, Webster I (2001) Porewater flow in permeable sediments. In: Boudreau BP, Jørgensen BB (eds) *The benthic boundary layer: Transport processes and biogeochemistry*. Oxford University Press, New York
- Huettel M, Ziebis W, Forster S (1996) Flow-induced uptake of particulate matter in permeable sediments. *Limnology and Oceanography* 41: 309-322
- Hume TM, Snelder T, Weatherhead M, Liefting R (2007) A controlling factor approach to estuary classification. *Ocean & Coastal Management* 50: 905-929
- Hummel H (1985) Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* 19: 52-76
- Iglesias JIP, Navarro E, Jorna PA, Armentia I (1992) Feeding, particle selection and absorption in cockles *Cerastoderma-edule* (L.) exposed to variable conditions of food concentration and quality. *Journal of Experimental Marine Biology and Ecology* 162: 177-198
- Jassby AD, Cloern JE, Powell TM (1993) Organic carbon sources and sinks in San Francisco Bay: Variability induced by river flow *Marine Ecology Progress Series* 95: 39-54
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. In: Blaxter JHS, Southward AJ, Tyler PA (eds) *Advances in Marine Biology*, Vol 34, pp 201-+
- Joint IR (1978) Microbial production of an estuarine mudflat. *Estuarine and Coastal Marine Science* 7: 185-195
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69: 373-386
- Jones H, Pilditch C, Bruesewitz D, Lohrer A (2011) Sedimentary environment influences the effect of an infaunal suspension feeding bivalve on estuarine ecosystem function. *PLoS ONE* 6

- Jones H, Pilditch C, Hamilton D, Bryan K (under review) Transfer of energy from microphytobenthos to higher trophic levels facilitated by infaunal suspension feeding bivalve in a shallow estuary. *Marine & Freshwater Research*
- Jumars PA, Wheatcroft RA (1989) Response of benthos to changing food quality, with a focus on deposit feeding and bioturbation. John Wiley & Sons Ltd, Chichester
- Kaplan EH, Welker JR, Kraus MG (1974) Some effects of dredging on population of macrobenthic organisms. *Fishery Bulletin* 72: 445-480
- Kelly JR, Berounsky VM, Nixon SW, Oviatt CA (1985) Benthic-pelagic coupling and nutrient cycling across an experimental eutrophication gradient. *Marine Ecology-Progress Series* 26: 207-219
- Kennish MJ (2002) Environmental threats and environmental future of estuaries. *Environmental Conservation* 29: 78-107
- Kimmerer WJ (2002) Physical, biological, and management responses to variable freshwater flow into the San Francisco estuary. *Estuaries* 25: 1275-1290
- Klute A, Dirksen C (1986) Hydraulic conductivity and diffusivity: Laboratory methods. In: Klute A (ed) *Methods of soil analysis, part one, physical and mineralogical methods* ASA and SSSA, Madison, Wisconsin USA, pp 687-732
- Kristensen E, Blackburn TH (1987) The fate of organic-carbon and nitrogen in experimental marine sediment systems-influence of bioturbation and anoxia. *Journal of Marine Research* 45: 231-257
- Kristensen E, Kostka JE (2005) Macrofaunal burrows and irrigation in marine sediment: Microbiological and biogeochemical interactions *Interactions Between Macro- and Microorganisms in Marine Sediments*. AGU, Washington, DC, pp 125-157
- Lelieveld SD, Pilditch CA, Green MO (2004) Effects of deposit-feeding bivalve (*Macomona liliana*) density on intertidal sediment stability. *New Zealand Journal of Marine and Freshwater Research* 38: 115-128
- Levin LA, Boesch DF, Covich A, Dahm C, Erseus C, Ewel KC, Kneib RT, Moldenke A, Palmer MA, Snelgrove P, Strayer D, Weslawski JM (2001) The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* 4: 430-451
- Levinton JS (1991) Variable feeding-behavior in 3 species of *Macoma* (Bivalvia, Tellinacea) as a response to water-flow and sediment transport. *Marine Biology* 110: 375-383
- Levinton JS, DeWitt TH (1989) Relation of particle-size spectrum and food abundance to particle selectivity in the mud snail *Hydrobia totteni*; (Prosobranchia: Hydrobiidae). *Marine Biology* 100: 449-454

- Lin J, Hines AH (1994) Effects of suspended food availability on the feeding mode and burial depth of the Baltic clam, *Macoma balthica*. *Oikos* 69: 28-36
- Lohrer AM, Thrush SF, Hewitt JE, Berkenbusch K, Ahrens M, Cummings VJ (2004) Terrestrially derived sediment: response of marine macrobenthic communities to thin terrigenous deposits. *Marine Ecology-Progress Series* 273: 121-138
- Lohrer AM, Thrush SF, Hunt L, Hancock N, Lundquist C (2005) Rapid reworking of subtidal sediments by burrowing spatangoid urchins. *Journal of Experimental Marine Biology and Ecology* 321: 155-169
- Lopez GR, Levinton JS (1987) Ecology of deposit-feeding animals in marine-sediments. *Quarterly Review of Biology* 62: 235-260
- Lundquist CJ, Pilditch CA, Cummings VJ (2004) Behaviour controls post-settlement dispersal by the juvenile bivalves *Austrovenus stutchburyi* and *Macomona liliana*. *Journal of Experimental Marine Biology and Ecology* 306: 51-74
- Macintyre HL, Cullen JJ (1995) Fine-scale vertical resolution of chlorophyll and photosynthetic parameters in shallow-water benthos *Marine Ecology Progress Series* 122: 227-237
- Marcus NH, Schmidt-Gengenbach J (1986) Recruitment of individuals into the plankton: The importance of bioturbation. *Limnology and Oceanography* 31: 206-210
- Marinelli RL (1992) Effects of polychaetes on silicate dynamics and fluxes in sediments- importance of species, animal activity and polychaete effects on benthic diatoms. *Journal of Marine Research* 50: 745-779
- Marinelli RL, Williams TJ (2003) Evidence for density-dependent effects of infauna on sediment biogeochemistry and benthic-pelagic coupling in nearshore systems. *Estuarine Coastal and Shelf Science* 57: 179-192
- Meysman FJR, Galaktionov ES, Middelburg JJ (2005) Irrigation patterns in permeable sediments induced by burrow ventilation: a case study of *Arenicola marina*. *Marine Ecology-Progress Series* 303: 195-212
- Meysman FJR, Middelburg JJ, Heip CHR (2006) Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology & Evolution* 21: 688-695
- Miller DC, Bock MJ, Turner EJ (1992) Deposit and suspension feeding in oscillatory flows and sediment fluxes. *Journal of Marine Research* 50: 489-520
- Milliman JD, Meade RH (1983) World-wide delivery of river sediment to the oceans. *Journal of Geology* 91: 1-21

- Ministry of Primary Industries (2012) Commercial fishing. Ministry of Primary Industries, Wellington, New Zealand
- Needham HR, Pilditch CA, Lohrer AM, Thrush SF (2010) Habitat dependence in the functional traits of *Austrohelice crassa*, a key bioturbating species Marine Ecology-Progress Series, pp 179-193
- Nixon SW, Ammerman JW, Atkinson LP, Berounsky VM, Billen G, Boicourt WC, Boynton WR, Church TM, Ditoro DM, Elmgren R, Garber JH, Giblin AE, Jahnke RA, Owens NJP, Pilson MEQ, Seitzinger SP (1996) The fate of nitrogen and phosphorus at the land-sea margin of the North Atlantic Ocean. Biogeochemistry 35: 141-180
- Norkko A, Thrush S, Hewitt J, Cummings V, Norkko J, Ellis J, Funnell G, Schultz D, MacDonald I (2002) Smothering of estuarine sandflats by terrigenous clay: the role of wind-wave disturbance and bioturbation in site-dependent macrofaunal recovery. Marine Ecology-Progress Series 234: 23-41
- Norkko J, Hewitt JE, Thrush SF (2006) Effects of increased sedimentation on the physiology of two estuarine soft-sediment bivalves, *Austrovenus stutchburyi* and *Paphies australis*. Journal of Experimental Marine Biology and Ecology 333: 12-26
- Nowicki BL, Nixon SW (1985) Benthic community metabolism in a coastal lagoon ecosystem. Marine Ecology Progress Series 22: 21-30
- Olafsson EB (1986) Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: A field experiment. Journal of Animal Ecology 55: 517-526
- Orfanidis S, Panayotidis P, Stamatis N (2001) Ecological evaluation of transitional and coastal waters: a marine benthic macrophytes-based model. Mediterr. Mar. Sci. 2: 45-65
- Ostroumov SA (2005) Suspension-Feeders as Factors Influencing Water Quality in Aquatic Ecosystems. In: Dame R, Olenin S (eds) The Comparative Roles of Suspension-Feeders in Ecosystems. Springer Netherlands, pp 147-164
- Parsons R, T, Maita Y, Lalli M, C (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press Ltd, Oxford, England
- Peterson CH (1985) Patterns of lagoonal bivalve mortality after heavy sedimentation and their paleoecological significance. Paleobiology 11: 139-153
- Pilditch CA, Emerson CW, Grant J (1997) Effect of scallop shells and sediment grain size on phytoplankton flux to the bed. Continental Shelf Research 17: 1869-1885

- Plantecuny MR, Bodoy A (1987) Biomass and primary production of phytoplankton and microphytobenthos in a sheltered and an exposed beach (Gulf of Fos, France). *Oceanologica Acta* 10: 223-237
- Polerecky L, Volkenborn N, Stief P (2006) High temporal resolution oxygen imaging in bioirrigated sediments. *Environmental Science & Technology* 40: 5763-5769
- Precht E, Huettel M (2003) Advective pore-water exchange driven by surface gravity waves and its ecological implications. *Limnology and Oceanography* 48: 1674-1684
- Precht E, Huettel M (2004) Rapid wave-driven advective pore water exchange in a permeable coastal sediment. *Journal of Sea Research* 51: 93-107
- Pridmore RD, Thrush SF, Hewitt JE, Roper DS (1990) Macrobenthic community composition of six intertidal sandflats in Manukau Harbour, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 24: 81-96
- Pritchard D (1967) What is an estuary: physical view point. In: Lauff GH (ed) *Estuaries*. AAAS, Washington DC, pp 3-5
- Putman RJ (1995) Ethical considerations and animal welfare in ecological field studies. *Biodiversity & Conservation* 4: 903-915
- Rhoads DC (1982) The influence of deposit-feeding organisms on sediment stability and community trophic structure *Current Contents/Agriculture Biology & Environmental Sciences*: 16-16
- Rocha C (2008) Sandy sediments as active biogeochemical reactors: compound cycling in the fast lane. *Aquatic Microbial Ecology* 53: 119-127
- Rodil IF, Lohrer AM, Chiaroni LD, Hewitt JE, Thrush SF (2011) Disturbance of sandflats by thin terrigenous sediment deposits: consequences for primary production and nutrient cycling. *Ecological Applications* 21: 416-426
- Romero LM (2004) Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology & Evolution* 19: 249-255
- Roper DS, Hickey CW (1994) Population structure, shell morphology, age and condition of the freshwater mussel *Hyridella menziesi* (Unionacea: Hyriidae) from seven lake and river sites in the Waikato River system. *Hydrobiologia* 284: 205-217
- Safi KA, Hewitt JE, Talman SG (2007) The effect of high inorganic seston loads on prey selection by the suspension-feeding bivalve, *Atrina zelandica*. *Journal of Experimental Marine Biology and Ecology* 344: 136-148
- Seitz RD, Lipcius RN, Olmstead NH, Seebo MS, Lambert DM (2006) Influence of shallow-water habitats and shoreline development on abundance, biomass, and diversity of benthic prey and predators in Chesapeake Bay. *Marine Ecology Progress Series* 326: 11-27

- Sun M-Y, Lee C, Aller RC (1993) Laboratory studies of oxic and anoxic degradation of chlorophyll *a* in Long Island Sound sediments. *Geochimica Et Cosmochimica Acta* 57: 147-157
- Sun M-Yi, Aller RC, Lee C, Wakeham SG (2002) Effects of oxygen and redox oscillation on degradation of cell-associated lipids in surficial marine sediments. *Geochimica Et Cosmochimica Acta* 66: 2003-2012
- Taghon GL, Jumars PA (1984) Variable ingestion rate and its role in optimal foraging behaviour of marine deposit feeders. *Ecology* 65: 549-558
- Thrush SF, Hewitt JE, Cummings V, Ellis JI, Hatton C, Lohrer A, Norkko A (2004) Muddy waters: elevating sediment input to coastal and estuarine habitats. *Frontiers in Ecology and the Environment* 2: 299-306
- Thrush SF, Hewitt JE, Norkko A, Cummings VJ, Funnell GA (2003) Macrobenthic recovery processes following catastrophic sedimentation on estuarine sandflats. *Ecological Applications* 13: 1433-1455
- Thrush SF, Hewitt JE, Pridmore RD, Cummings VJ (1996) Adult/juvenile interactions of infaunal bivalves: Contrasting outcomes in different habitats. *Marine Ecology-Progress Series* 132: 83-92
- Thrush SF, Pridmore RD, Bell RG, Cummings VJ, Dayton PK, Ford R, Grant J, Green MO, Hewitt JE, Hines AH, Hume TM, Lawrie SM, Legendre P, McArdle BH, Morrissey D, Schneider DC, Turner SJ, Walters RA, Whitlatch RB, Wilkinson MR (1997) The sandflat habitat: scaling from experiments to conclusions. *Journal of Experimental Marine Biology and Ecology* 216: 1-9
- Townsend M, Thrush SF, Carlines MJ (2011) Simplifying the complex: an 'Ecosystem Principles Approach' to goods and services management in marine coastal ecosystems. *Marine Ecology-Progress Series* 434: 291-301
- Turk TR, Risk MJ (1981) Effect of sedimentation of infaunal invertebrate populations of Cobequid Bay, Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 642-648
- Varela M, Penas E (1985) Primary production of benthic microalgae in an intertidal sand flat of the Ria de Arosa, NW Spain. *Marine Ecology Progress Series* 25: 111-119
- Volkenborn N, Hedtkamp SIC, van Beusekom JEE, Reise K (2007) Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina*) on physical and chemical sediment properties and implications for intertidal habitat succession. *Estuarine Coastal and Shelf Science* 74: 331-343
- Volkenborn N, Meile C, Polerecky L, Pilditch C, Norkko A, Norkko J, Hewitt J, Thrush S, Wetthey D, Woodin S (under review) Intermittent bioirrigation and oxygen dynamics in permeable sediments: An experimental and modeling study of three tellinid bivalves

- Volkenborn N, Polerecky L, Wethey DS, Woodin SA (2010) Oscillatory porewater bioadvection in marine sediments induced by hydraulic activities of *Arenicola marina*. *Limnology and Oceanography* 55: 1231-1247
- Waldbusser GG, Marinelli RL (2006) Macrofaunal modification of porewater advection: role of species function, species interaction, and kinetics. *Marine Ecology-Progress Series* 311: 217-231
- Ward E, Shumway S (2004) Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves. *Journal of Experimental Marine Biology and Ecology* 300: 83-130
- Wethey DS, Woodin SA (2005) Infaunal hydraulics generate porewater pressure signals. *Biological Bulletin* 209: 139-145
- Wethey DS, Woodin SA, Volkenborn N, Reise K (2008) Porewater advection by hydraulic activities of lugworms, *Arenicola marina*: A field, laboratory and modeling study. *Journal of Marine Research* 66: 255-273
- Wong WH, Cheung SG (1999) Feeding behaviour of the green mussel, *Perna viridis* (L.): Responses to variation in seston quantity and quality. *Journal of Experimental Marine Biology and Ecology* 236: 191-207
- Woodin SA, Wethey DS (2009) Arenicolid behaviors: similarity of *Arenicola marina* and *Abarenicola pacifica*. In: Maciolek NJ, Blake JA (eds) *Proceedings of the 9th International Polychaete Conference*, pp 447-456
- Woodin SA, Wethey DS, Hewitt JE, Thrush SF (2012) Small scale terrestrial clay deposits on intertidal sandflats: Behavioral changes and productivity reduction. *Journal of Experimental Marine Biology and Ecology* 413: 184-191
- Woodin SA, Wethey DS, Volkenborn N (2010) Infaunal hydraulic ecosystem engineers: cast of characters and impacts. *Integrative and Comparative Biology* 50: 176-187
- Ziebis W, Huettel M, Forster S (1996) Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds. *Marine Ecology-Progress Series* 140: 227-237

A.1: Pressure records for each treatment

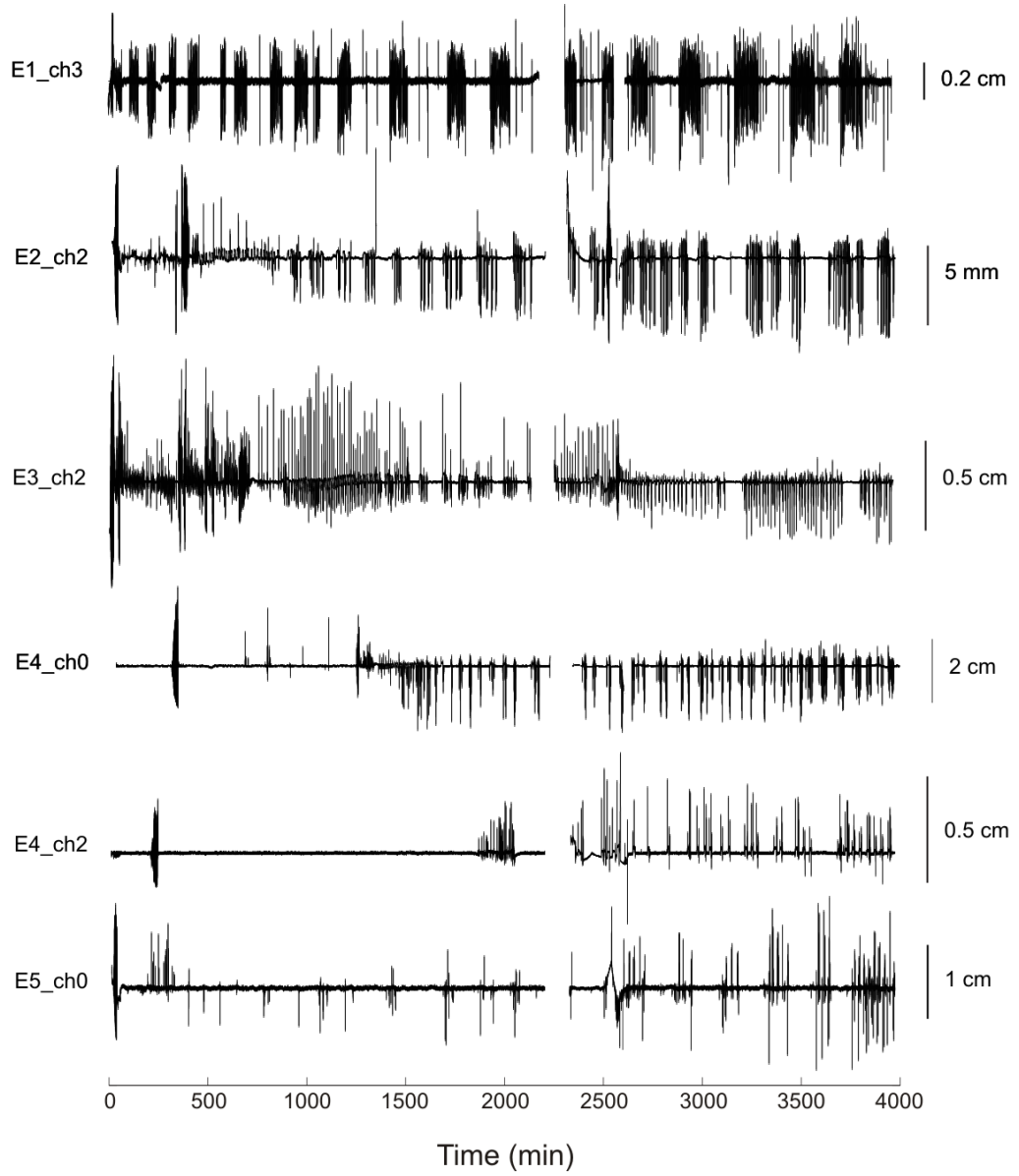


Figure A.1. 1: Pressure records used from the control treatments showing the experiment (E1-E5) and pressure sensor channel (ch) on the right, the pressure height on the right and the time (min) along the bottom.

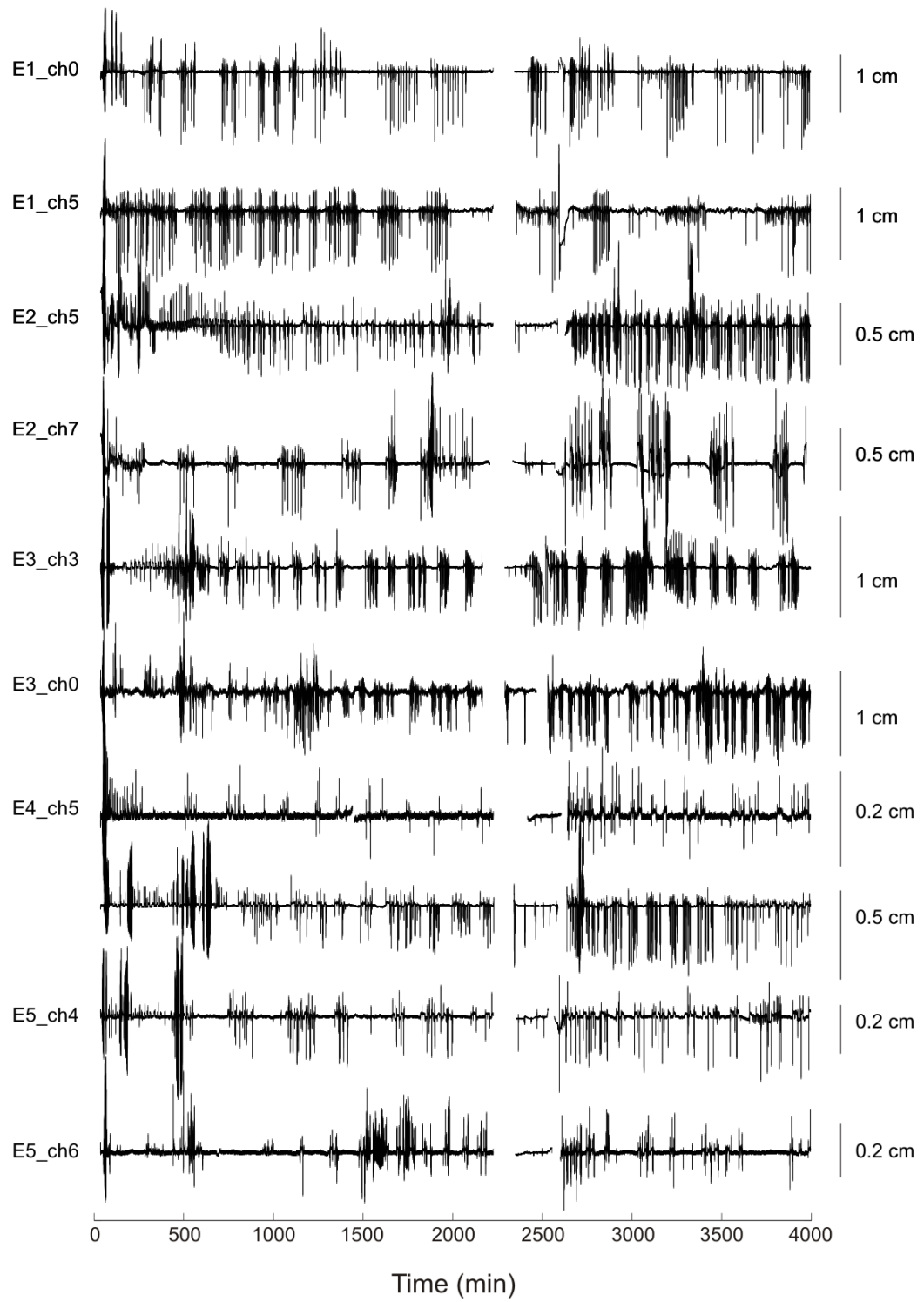


Figure A.1. 2: Pressure records used from the low treatments showing the experiment (E1-E5) and pressure sensor channel (ch) on the right, the pressure height on the right and the time (min) along the bottom.

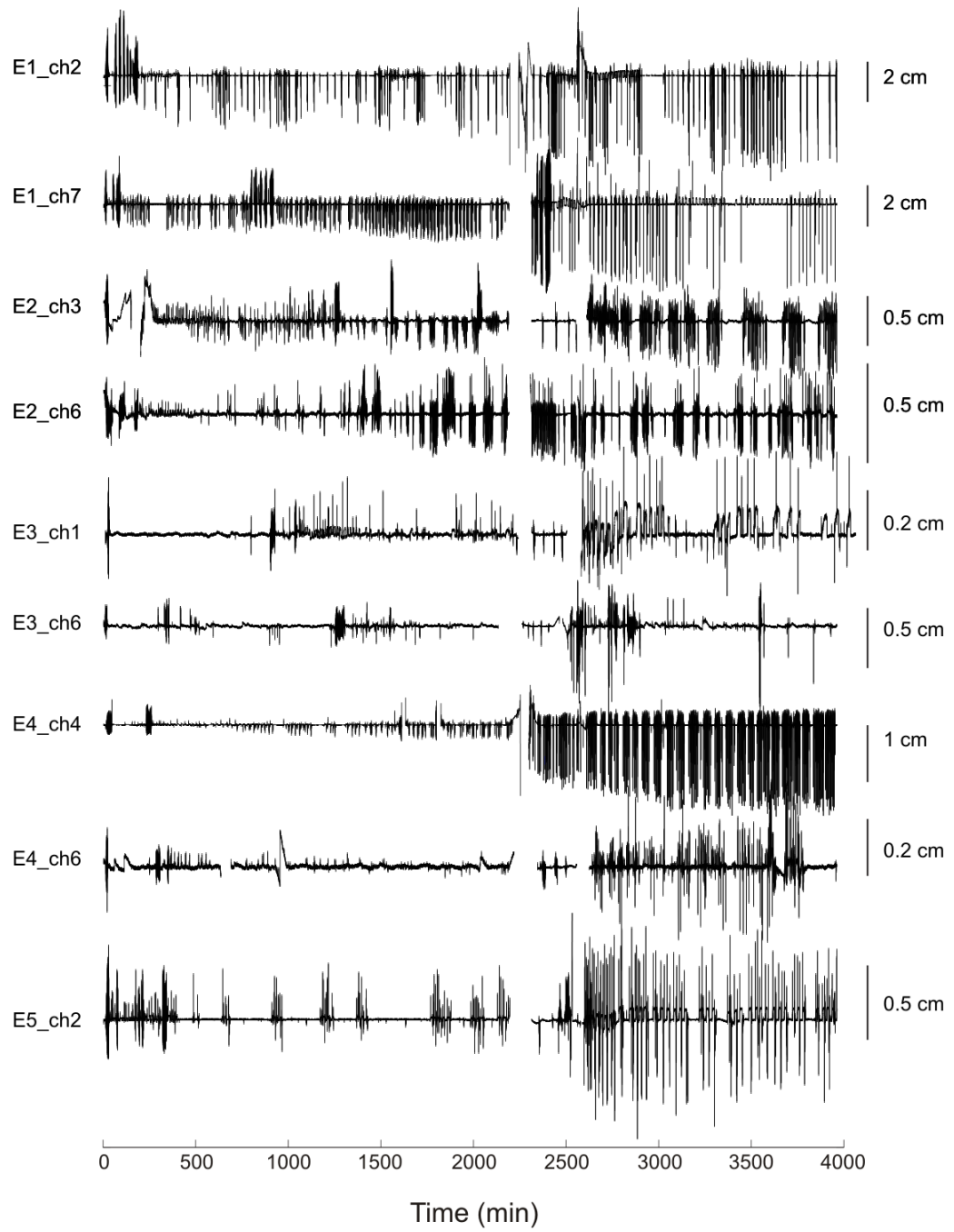


Figure A.1. 3: Pressure records used from the mixed treatments showing the experiment (E1-E5) and pressure sensor channel (ch) on the right, the pressure height on the right and the time (min) along the bottom.

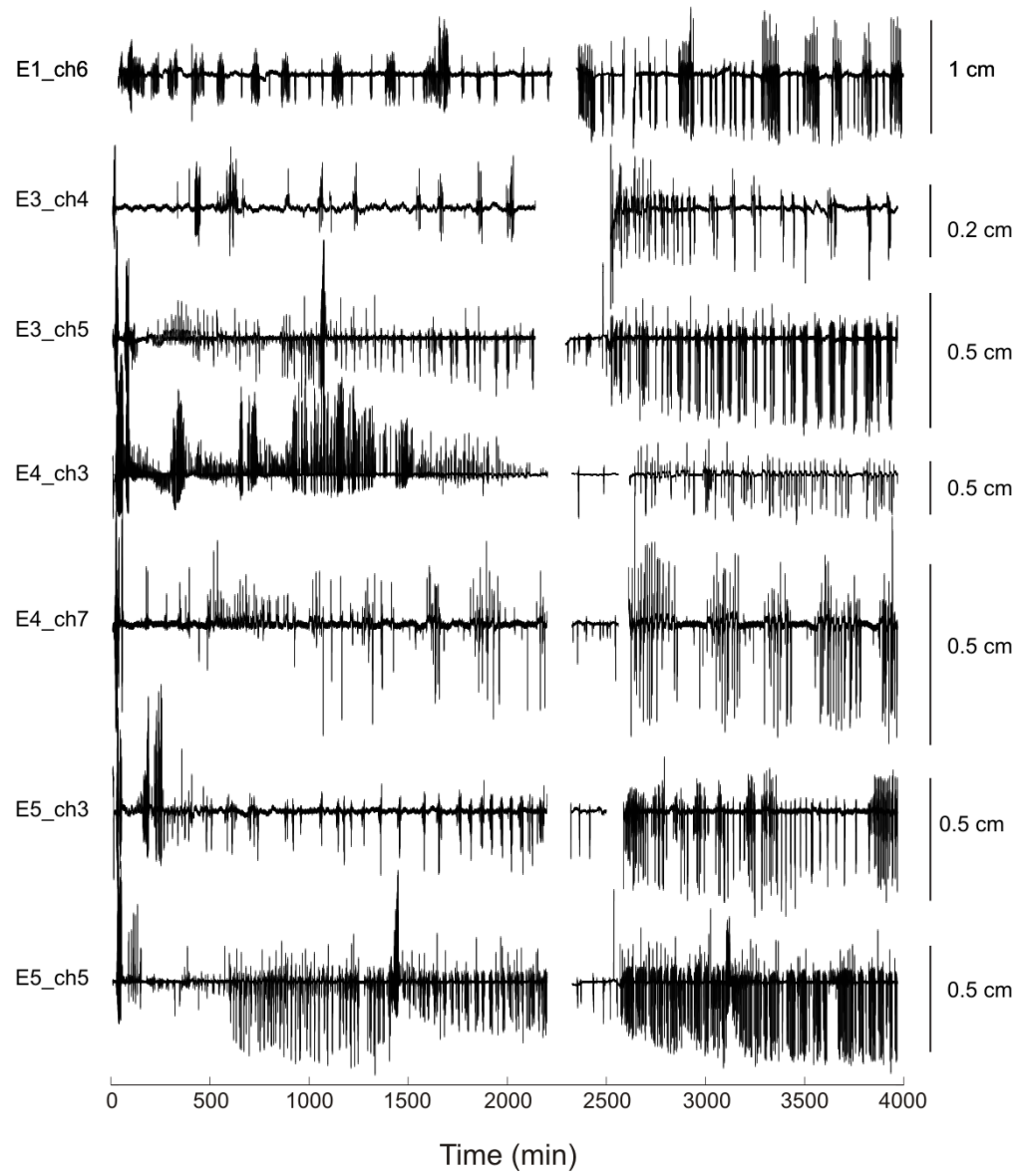


Figure A.1. 4: Pressure records used from the high treatments showing the experiment (E1-E5) and pressure sensor channel (ch) on the right, the pressure height on the right and the time (min) along the bottom.